

RECORDS OF THE AUSTRALIAN MUSEUM

Volume 71

Number 4

24 July 2019

Towards a systematic revision of the eastern Australian land snail
Austrochloritis Pilsbry, 1891 (Eupulmonata, Camaenidae):
re-description of its type species, *A. porteri* (Cox, 1866)

by

Michael Shea and Frank Köhler

The flint artefacts from two workshops at Wadi el-Sheikh,
Eastern Desert, Egypt

by

Stan Florek, Thomas Hikade and Sarah Carter

Species of Heterolepismatinae (Zygentoma: Lepismatidae) found on
some remote eastern Australian Islands

by

Graeme B. Smith and Andrew Mitchell



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Volume 71 Number 4

Published (print and online) 24 July 2019

Price: AU\$50.00

Printed by Rodenprint Pty Ltd, Sydney

ISSN 0067-1975 (print)

ISSN 2201-4349 (online)

The Australian Museum is a statutory authority of, and principally funded by, the NSW State Government.



Cover image—Upside Down Flies of the family Neurochaetidae McAlpine 1978 have the curious habit of facing downwards and walking sideways and backwards. “Populations of *Neurochaeta inversa* McAlpine 1978 have always been found in association with the araceous plant *Alocasia macrorrhizos* (Linné) G. Don (known as Cunjevoi or Spoon Lily), growing in its original habitat. The flies have not yet been found on cultivated examples, which are common in Sydney gardens. So far they have not been found on any other plant, even as a casual visitor, despite much sweeping of vegetation for insects near the *Alocasia*. The life cycle is ... intimately connected with this plant ... (McAlpine, 1978:291; all of McAlpine’s peer-reviewed publications are listed in this issue).

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<https://doi.org/10.3853/issn.2201-4349>

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Towards a Systematic Revision of the Eastern Australian Land Snail *Austrochloritis* Pilsbry, 1891 (Eupulmonata, Camaenidae): Re-description of its Type Species, *A. porteri* (Cox, 1866)

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ABSTRACT. *Helix porteri* Cox, 1866 is the type species of *Austrochloritis* Pilsbry, 1891, a speciose genus of camaenid land snail with a known range in eastern Australia stretching from Wilson's Promontory in Victoria to southeastern Queensland. This species was first described based on material from two locations in New South Wales, "Upper Clarence River at Guy Faux Station" and "Upper Richmond River, at Cowlong". These two locations are about 230 km apart from each other while all type material is considered to be lost. Comparative morpho-anatomy of specimens collected in the proximity of both type localities shows that the original concept of *Helix porteri* is based on two distinct species. Here we designate a neotype for this species from the Upper Richmond River area and provide a detailed redescription in order to remove any ambiguity about the identity of *Austrochloritis porteri*. Material from the vicinity of the second site mentioned in the original description of *H. porteri*, Guy Fawkes Station, is identified as *Austrochloritis speculoris* Shea & Griffiths, 2010. We describe key diagnostic features distinguishing both species.

Introduction

Austrochloritis Pilsbry, 1891 is probably the most speciose land snail genus in eastern Australia comprising 34 currently accepted species (Stanisic *et al.*, 2010). These species are overall similar externally, having rather small, depressed and hairy shells of dull brown colour. Given their rather inconspicuous appearance, *Austrochloritis* species have historically not received the same attention of taxonomists that other land snail groups with more distinct looking shells may have enjoyed. Yet, the systematic concept of *Austrochloritis* has changed significantly since its original description. Still, the currently preferred classification introduced by Stanisic *et al.* (2010) is not without difficulties, which arise from the subjectivity and inconsistencies of 150

years of changing taxonomic treatments and the prevailing lack of critical anatomical and molecular phylogenetic data, which is essential to achieve a more objective systematic classification. *Austrochloritis* was described as a subgenus in *Chloritis* Beck, 1837, for the type species *Helix porteri* Cox, 1866, and has subsequently become a catch-all for uniform brownish bristle snails from eastern Australia and even New Guinea (e.g., Pilsbry, 1891: 262–265; Gude, 1906; Iredale, 1938; Zilch, 1966). Iredale (1933) argued that the presence of periostracal setae alone was not a sufficient character to unify all Australian "chloritids" under one genus name, let alone the New Guinean species, and successively allocated Australian species into several genera based on assessments of additional shell characters, such as protoconch sculpture, the elevation of the shell spire, and the size and shape of the

Keywords: Stylommatophora; taxonomic revision; reproductive anatomy; shell morphology; Hadrinae

Taxonomic registration: (LSID publication) <http://zoobank.org/BC469398-0572-492D-A29F-37F5BFF9199C>

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Received: 15 February 2019 **Accepted:** 23 May 2019 **Published:** 24 July 2019 (in print and online simultaneously)

Publisher: The Australian Museum, Sydney, Australia (a statutory authority of, and principally funded by, the NSW State Government)

Citation: Shea, Michael, and Frank Köhler. 2019. Towards a systematic revision of the eastern Australian land snail *Austrochloritis* Pilsbry, 1891 (Eupulmonata, Camaenidae): re-description of its type species, *A. porteri* (Cox, 1866). *Records of the Australian Museum* 71(4): 111–120.

<https://doi.org/10.3853/j.2201-4349.71.2019.1699>

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shell. Iredale (1938) elevated *Austrochloritis* to full genus rank and recognized fourteen species as its members, whose combined distribution spanned the Australian east coast from Cape York to northern New South Wales. Subsequently, Iredale (1943) added three more species-group taxa with his usual casual flare. Anatomical data has been published on very few species so far, often associated with uncertain species identifications. Hedley (1890) first figured the jaw, radula and genitalia of what he considered to be *Helix porteri* from Upper Nerang Creek near Brisbane, Queensland (28°12'S 153°14'E). Pilsbry (1894) also published a drawing of the reproductive anatomy of this species without specifying the origin of the examined material. Much later, Solem (1979) presented a detailed description of the reproductive anatomy of what he identified as *Austrochloritis disjuncta* from the Barrington Tops and *A. victoriae* from Wilson's Promontory in Victoria. Based on his observations of a largely consistent reproductive anatomy in both species, Solem (1979) concluded that *Chloritobadistes* Iredale, 1933, which he considered to be *nomen nudum* for the lack of a diagnosis in the original description, was identical with *Austrochloritis*. In a molecular phylogeny of the eastern Australian Camaenidae, Huggall & Stanisic (2011) found *Austrochloritis* as delineated before 2010 to be polyphyletic. Anticipating this result, Stanisic *et al.* (2010) described several new genera, such as *Aetholitis* Stanisic, 2010 and *Trachygenia* Stanisic, 2010, to accommodate species that are phylogenetically clearly distinct from the type species *A. porteri*. However, the re-alignment of the genus boundaries has been proposed in spite of rather poor knowledge of the type species *A. porteri*. No type material is known to exist that might aid its correct identification while two distinct localities are given as type locality in the original description that are about 230 km apart from each other. According to the current systematic treatment by Stanisic *et al.* (2010), most *Austrochloritis* species are narrow-range endemics and based on the average size of species ranges in this genus it is unlikely that the two localities mentioned in the original description harbour the same species. It is therefore probable that the original description of *Helix porteri* was based on material representing more than a single species. In order to remove prevailing ambiguity about the identity of *Austrochloritis porteri*, we here designate a neotype and re-describe its morpho-anatomy as a first step towards a systematic revision of the entire genus.

Materials and methods

This study is based on examination of relevant material housed in the collections of the Australian Museum in Sydney (AM) and the Queensland Museum in Brisbane (QM), including historic and newly collected material, both wet and dry.

A Leica MZ8 stereo microscope with a drawing apparatus was used to examine the reproductive anatomy of ethanol preserved samples by means of anatomical dissection. Bodies were removed from shells prior to dissection and shells were photographed. Shell height (H) and diameter (D) were measured with callipers accurate to 0.5 mm. We also counted the number of whorls (N) as shown by Köhler (2011). Selected shells were cleaned by gently brushing in warm soapy water, dried, mounted on carbon specimen tabs, and coated with gold for electron scanning microscopy.

Abbreviations used

Repositories: AM, Australian Museum, Sydney; NHMUK, Natural History Museum, London (UK); NMV, National Museum of Victoria, Melbourne; QM, Queensland Museum, Brisbane; SMF, Naturmuseum Senckenberg, Frankfurt (Germany); ZMB, Museum für Naturkunde, Berlin (Germany). *Shell measurements*: D, diameter; H, height. *Geography*: Ck, creek; Hwy, highway; Mt, Mount; NP, National Park; nr, near; Rd, road; SF, State Forest.

Systematics

Gastropoda

Stylommatophora

Family Camaenidae Pilsbry, 1895

Genus *Austrochloritis* Pilsbry, 1891 (type species: *Helix porteri* Cox, 1866, by original designation).

Austrochloritis Pilsbry, 1891 (in Pilsbry, 1890–1891): 262–263; Pilsbry, 1894 (in Pilsbry, 1893–1895): 121–122, pl. 28, figs 1–2; Gude, 1906: 114–115; Iredale, 1938: 93–95, 1943: 64–65; Solem, 1979: 120–125; Smith, 1992: 116–118; Stanisic *et al.*, 2010: 378–392, 535–537; Stanisic *et al.* 2018: 258, 557.

Taxonomic history

Originally described as infrageneric taxon in *Chloritis*, *Austrochloritis* was elevated to full genus rank by Iredale (1938). Next to the type species, *A. porteri* (Cox, 1866), Pilsbry's (1891) original definition of *Austrochloritis* included several eastern Australian species, such as *Helix spinei* Cox, 1868 (now *Mussonena spinei*), *H. mansueta* Reeve, 1854 (now *Moretonistes mansueta*), *H. blackalli* Brazier, 1875 (now *Gloreugenia blackalli*), *H. buxtoni* Brazier, 1880 (now *Patrubella buxtoni*), *H. brevipila* Pfeiffer, 1849 (now *Austrochloritis brevipila*), *H. aridorum* Cox, 1866 (now *Neveritis aridorum*) as well as two species from New Guinea (refer to Stanisic *et al.*, 2010 for the currently accepted taxonomy of eastern Australian Camaenidae). Subsequently, Gude (1906), Iredale (1938, 1943) and Stanisic *et al.* (2010) described additional species. Iredale (1938) and Stanisic *et al.* (2010) also transferred several species to other genera. Solem (1979) misidentified a then undescribed species of *Austrochloritis* as *Chloritobadistes victoriae* (Cox, 1868) and, based on this misidentification, considered *Chloritobadistes* Iredale, 1933 as a synonym of *Austrochloritis*. Rectifying this mistake, Stanisic *et al.* (2010, 2018) removed *Chloritobadistes* from the synonymy of *Austrochloritis* and described the mistaken and up till then unnamed species as *A. beecheyi* Shea & Griffiths, 2018. According to the latest taxonomic treatment of Stanisic *et al.* (2010, 2018), the genus comprises 34 currently accepted species. We agree with the Stanisic *et al.* (2010) treatment of *Chloritobadistes* as an available name in accordance with Art. 13.3 of the Code (ICZN 1999), because the original description of Iredale (1933: 49, 58) contains, although a very brief, diagnosis ("In shell features it agrees with the shells of "*Badistes*" = *Meridolum* ante, but bears hairs. It has a smooth apex...") as well as a type species designation.

Diagnosis

Shell. Small to large in size ($D = 14\text{--}24\text{ mm}$), subdiscoidal, subglobose, turbinate or trochoidal with almost flat to moderately elevated spire ($H = 4\text{--}15\text{ mm}$), whorls rounded, shouldered, subangulate or keeled, sutures moderately to strongly impressed; umbilicus from moderately open to partially closed, with V-shaped profile; protoconch sculpture of dense to scattered pustulose radial ridges; teleoconch sculpture smooth or with regular radial corrugations and overlying low rounded pustules that support periostracal setae, interstitial microsculpture of fine wavy periostracal ridgelets; lip unreflected to strongly reflected, usually with a distinct sulcus and associated swelling behind; body whorl slightly to strongly descending below whorl plane; lip white to dark reddish brown; colour pale yellow-brown to dark red-brown, with or without a single narrow spiral colour band at mid-whorl, rarely with umbilical colour patch.

External anatomy. Animal dark grey or black to orange-brown; retractable head wart near inner bases of ocular tentacles present, varying in size.

Reproductive anatomy. Penis with or without a penial sheath, internally with vergic papilla that may have a very elongated to short conical or blunt tip, open laterally and apically, or have one lobe fastened to the penis wall and another free lobe; inner penial wall supporting irregular longitudinal interlocking ridges and pustulations of various lengths; penial retractor muscle inserting near mid-epiphallus; epiphallus rather long with or without very short to rather long finger-like caecum; vas deferens entering head of epiphallus through simple pore; vagina with prominent longitudinal anastomosing pilasters, usually thickened around entrance decreasing in prominence apically; bursa copulatrix moderately long (equal to length of oviduct) to very long (longer than oviduct), with multi-folded or looped shaft (twice as long as oviduct, or longer), with oval shaped head, aligned against terminal end of spermoviduct; free oviduct short; hermaphroditic duct inserting into head of talon.

Comparative remarks

Austrochloritis is distinguished from other eastern Australian camaenids by the combination of pale to dark brown discoidal to turbinate to trochoidal shell with pustulose radial wrinkles on protoconch, closely spaced curved to straight to strap-like pointed periostracal setae on teleoconch and typical reproductive characters, such as a rather long bursa copulatrix with multi-folded or looped shaft and oval shaped head, aligned against terminal end of spermoviduct, a long epiphallus, usually with caecum, and a free vergic papilla of the penis.

Distribution

From SE Victoria (Wilson's Promontory and Mt Donna Buang) to SE Queensland (Mt Tamborine). Mainly coastal and sub-coastal, but ranging as far west as Warrumbungle Range in central New South Wales; from near sea level to altitudes of up to c. 1,700 m in the Snowy Mountains.

Austrochloritis porteri (Cox, 1866)

Helix porteri Cox, 1866: 373 [publ. 5 Sep]; Hedley, 1890: 249–250, pl. 15.

Chloritis (Austrochloritis) porteri.—Pilsbry, 1891 (in 1890–1891): 263, pl. 58, figs 23–24; Pilsbry, 1894 (in 1893–95): 121, pl. 28, figs 1–4; Zilch, 1966: 299.

Austrochloritis porteri.—Iredale, 1938: 94; Stanisic *et al.* 2010: 390.

Material examined

Type material. Neotype, herein designated, AM C.24556 from New South Wales, Upper Richmond River, Booyong, Pearces Ck, $28^{\circ}45'00''\text{S}$ $153^{\circ}26'53''\text{E}$ (leg. 1906) (Fig. 1A).

Non-type material. NEW SOUTH WALES: Upper Richmond River, Booyong, Pearces Ck, $28^{\circ}45'00''\text{S}$ $153^{\circ}26'53''\text{E}$ (AM C.557014); Upper Richmond River, $28^{\circ}30'30''\text{S}$ $152^{\circ}59'\text{E}$ (AM C.334934–35); Wilson River, tributary of Richmond River, Booyong, $28^{\circ}44'53''\text{S}$ $153^{\circ}26'53''\text{E}$ (AM C.112291); Richmond River (AM C.33390, AM C.339397, AM C.334941, AM C.334943–45); 25 km NE of Kyogle, Wiangarie SF, off Forest Rd, $28^{\circ}23'23''\text{S}$ $153^{\circ}6'24''\text{E}$ (AM C.339394, AM C.339744); Whian Whian SF, Red Scrub Flora Reserve, $28^{\circ}38'12''\text{S}$ $153^{\circ}19'48''\text{E}$ (AM C.339391, AM C.339745); Whian Whian SF, Terania Ck, Mackays Rd, $28^{\circ}35'\text{S}$ $153^{\circ}19'\text{E}$ (AM C.339395–96, AM C.339743); E of Mullumbimby, Huonbrook, upper Coopers Ck, $28^{\circ}33'\text{S}$ $153^{\circ}21'\text{E}$ (AM C.334959); Mt Warning, track to summit, 50–100m from carpark, $28^{\circ}23'55''\text{S}$ $153^{\circ}16'59''\text{E}$ (AM C.463198, AM C.463214); Mt Warning, $28^{\circ}24'\text{S}$ $153^{\circ}16'11''\text{E}$ (AM C.136825); banks of the Richmond River at Casino, $28^{\circ}52'\text{S}$ $153^{\circ}03'\text{E}$ (AM C.137773); SE of Lismore, near Alstonville, Victoria Park, $28^{\circ}54'\text{S}$ $153^{\circ}24'30''\text{E}$ (AM C.363835); Byron Bay, $28^{\circ}39'\text{S}$ $153^{\circ}37'\text{E}$ (AM C.31218, AM C.339398); E of Lismore, Wollongbar, $28^{\circ}49'\text{S}$ $153^{\circ}24'\text{E}$ (AM C.334946); SW of Murwillumbah, Byangum, $28^{\circ}21'30''\text{S}$ $153^{\circ}21'37''\text{E}$ (AM C.334948, C.334950); Tweed River, $28^{\circ}18'\text{S}$ $153^{\circ}27'\text{E}$ (AM C.55539). QUEENSLAND: Lamington NP, Binna Burra, Bellbird Circuit, $28^{\circ}12'\text{S}$ $153^{\circ}11'\text{E}$ (AM C.363837, AM C.444258, AM C.363842–43, AM C.512604); Lamington NP, Binna Burra Guest House, $28^{\circ}11'46''\text{S}$ $153^{\circ}11'20''\text{E}$ (AM C.363837, AM C.363842–43, AM C.444258); Lamington NP, O'Reilly's Camp Ground, $28^{\circ}13'54''\text{S}$ $153^{\circ}08'01''\text{E}$ (AM C.129249); Numinbah Valley Rd, 1 km S of Natural Arch, $28^{\circ}14'21''\text{S}$ $153^{\circ}14'17''\text{E}$ (AM C.474737); NW of Murwillumbah, nr Springbrook, $28^{\circ}14'07''\text{S}$ $153^{\circ}16'38''\text{E}$ (AM C.444266); Currumbin Valley, $28^{\circ}08'\text{S}$ $153^{\circ}29'\text{E}$ (AM C.444267); Currumbin, 4 miles W of coast, $28^{\circ}8'\text{S}$ $153^{\circ}25'19''\text{E}$ (AM C.363858); Collins Gap, Mt Lindsay Hwy, $28^{\circ}20'\text{S}$ $152^{\circ}42'\text{E}$ (AM C.444259); Natural Bridge NP, $28^{\circ}13'\text{S}$ $153^{\circ}14'\text{E}$ (AM C.129279).

Nomenclatural and taxonomic remarks

The original type material could not be traced in the AM, nor in the QM, NMV, ZMB, SMF, NHMUK, and is considered lost. Cox's types have generally been deposited in the collection of the Australian Museum. Indeed, other historic shell material collected by both Porter and Macgillivray in northern NSW in or before 1866 is still extant in this collection. Repeated efforts by various persons (Alan Solem, John Stanisic, ourselves) to find type material at the AM or other institutions have been unsuccessful. No types are known or suspected to be kept in other museums. Zilch (1966) did not report any types to be held by the SMF.

The original description was based on material collected by two different collectors at two separate sites: "Upper Clarence River at Guy Faux Station (Porter)" and "Upper Richmond River, at Cowlong [...] (Macgillivray)". Using contemporary georeferenced materials, we have located these two sites with reasonable precision. The first site is Guy Fawkes Station, N of Ebor and W of Point Lookout within the uppermost Clarence River catchment (c. $30^{\circ}21'00''\text{S}$ $152^{\circ}22'12''\text{E}$). The second is NE of Lismore, S of Booyong (c. $28^{\circ}46'12''\text{S}$ $153^{\circ}25'12''\text{E}$) (Fig. 2). Both locations are about 230 km apart from each other. Since the type material was collected in 1866, the original forest cover that existed at this time has largely been destroyed through clearing for agriculture. However, we



Figure 1. Shells (front, top, and umbilical view). (A–C) *Austrochloritis porteri*: (A) neotype of *Helix porteri* AM C.24556 (NSW, Upper Richmond River); (B) AM C.575455 (NSW, Mt Warning); (C) AM C.512605 (Queensland, Lamington NP). (D–E) *Austrochloritis specularis*: (D) AM C.575464 (NSW, Point Lookout); (E) AM C.575456 (NSW, Cathedral Rock NP). Scale bar = 10 mm.

have examined material from as close to these two locations as possible and found that the *Austrochloritis* species found near one (Guy Fawkes) is not identical with that found near the other site (Cowlong) even though they are both similar in external appearance. It is not impossible to identify *A. porteri* among these two species based on the diagnosis given in the original description. In order to remove the uncertain identity of *Helix porteri* Cox, 1866, to stabilize this taxonomic name and to fix the type locality, we here designate a neotype in accordance with Art. 75 of The Code (ICZN, 1999) and provide an updated diagnosis.

Hedley (1890) and Pilsbry (1894) published descriptions and figures of the digestive and reproductive anatomy and attributed these to *A. porteri*. Hedley's (1890) material originated from near Brisbane, which is not very close to any of the two original locations. The whereabouts of Pilsbry's (1894) material have remained uncertain. Stanisić *et al.* (2010) reported the species to be distributed from SE of Lismore (Victoria Park, NSW) to W of Gold Coast (Springbrook, Qld). This distribution incorporates the second site mentioned in the original description (Cowlong), but not the first. By contrast, the species occurring at the first site, Guy Fawkes Station, has subsequently been described as *A. speculoris* Shea & Griffiths, 2010 (see below). To conserve the subsequent use of these two species names, we chose the neotype to come from close to site 2 (Cowlong).

Description

Shell (Fig. 1A–C, Fig. 3). Large ($D=14\text{--}24$ (average 17.8) mm, $H=10\text{--}15$ (average 12) mm; for $n = 34$ lots), subglobose to turbinate in shape with a low to moderately raised spire, with on average 4.25 rounded to sub-angulate whorl that increase in diameter, sutures moderately impressed; protoconch sculpture of scattered pustules and rugose pustulose radial ridges; teleoconch sculpture of low irregular growth lines with microsculpture of small crowded pustules, periostracal sculpture of crowded short curved setae, microsculpture of wavy periostracal ridgelets; end of last whorl descending below whorl plane; aperture moderately tilted from axis of coiling, with moderately thickened and reflected white outer lip with sulcus behind, columella slope about 45° ; umbilicus narrow and partially covered by reflected columella, V-shaped in profile; shell colour from pale reddish brown to dark reddish brown, with or without a narrow reddish brown spiral colour band at whorl periphery.

General anatomy. A retractable head wart is present at the inner bases of the ocular tentacles. Animal head-foot dark grey.

Reproductive anatomy (Fig. 4). Penis cylindrical, no penial sheath, inner penial wall with corrugated interlocking longitudinal pilasters, distally giving rise to longitudinal rows of interlocking pilasters; epiphallus cylindrical, about 1.5 to 2 times as long as penis, distal end with well-developed epiphallallic flagellum, broad at base, epiphallus tapering to very narrow toward apex, opening into penial lumen through a conical longitudinally grooved (Victoria Park and Binna Burra; Figs 4 D,F) to pustulose (Mt Warning; Fig. 4 E), free verge, opening laterally; penial retractor attached to mid-epiphallus; vas deferens entering head of epiphallus through single pore just below base of epiphallallic flagellum; vas deferens quite broad at its junction with apex of epiphallus but later tapering to a narrow tubule; vagina cylindrical, twice as long as penis, inner wall with prominent longitudinal

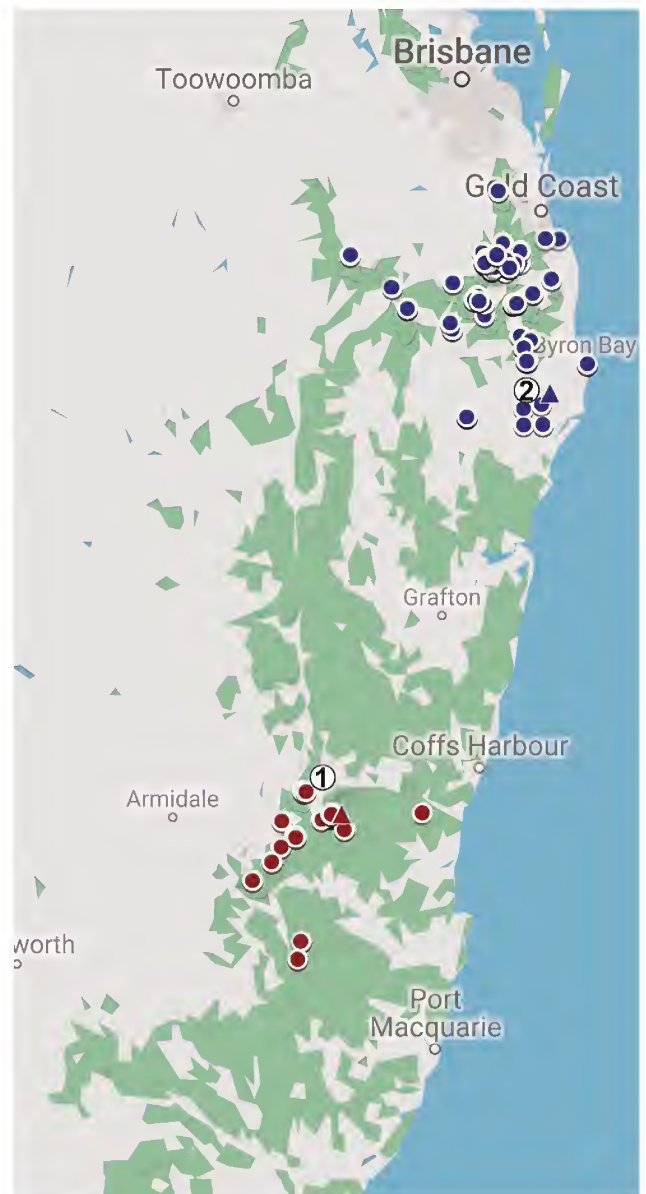


Figure 2. Occurrence records of *Austrochloritis porteri* (blue dots) and *A. speculoris* (red dots) from the malacological collection of the AM. Legend: blue triangle—type locality of *A. porteri* based on neotype AM C.24556, red triangle—type location of *A. speculoris*, original type locality of *Helix porteri*: 1—Guy Fawkes Station near Ebor; 2—Cowlong. Source of base map: Google Maps.

anastomising pilasters usually thickened around vaginal entrance; free oviduct very short; bursa copulatrix long and broad, particularly at its base, folded or kinked several times, about as long as spermoviduct (Victoria Park and Binna Burra; Figs 4A,C) to 1.5 times longer (Mt Warning; Fig. 4B), with inflated bulb-like head, aligning with base of albumen gland; hermaphroditic duct inserting into head of talon.

Distribution and ecology

Lives in subtropical rainforests from the Richmond River valley of NE NSW north to the upper Nerang Creek valley of SE Qld. Mainly found at altitudes of up to 900 m on basaltic bedrock; found under logs, rocks and inside sheaths of fallen palm leaves (Fig. 2).

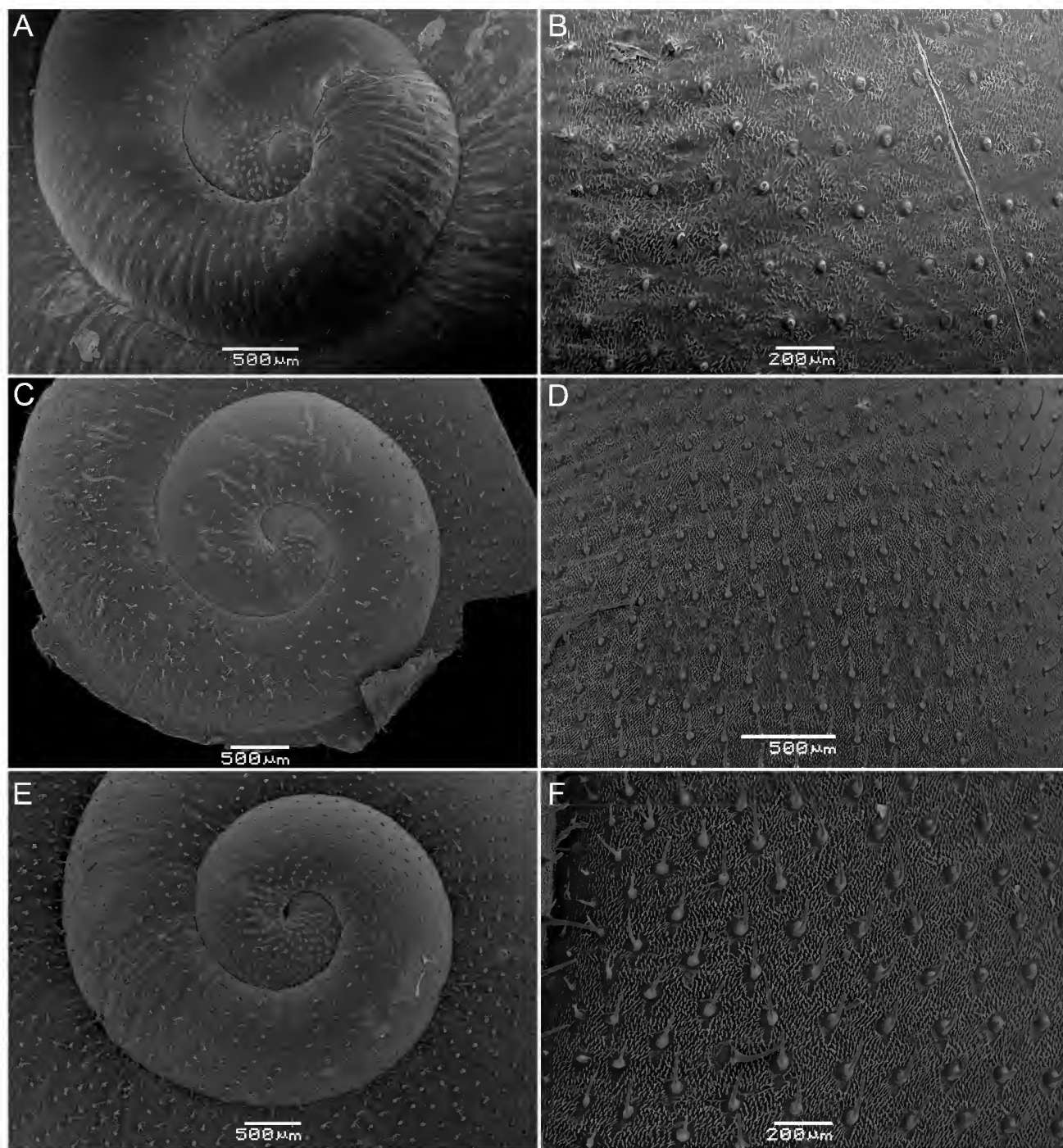


Figure 3. Scanning electron micrographs of shells of *Austrochloritis porteri* showing protoconch (left) and detail of teleoconch sculpture (right). (A, B) AM C.557014 (topotype, Upper Richmond River); (C, D) AM C.575262 (NSW, Mt Warning); (E, F) AM C.444258 (Queensland, Lamington NP). Scale bars = 0.2 or 0.5 mm.

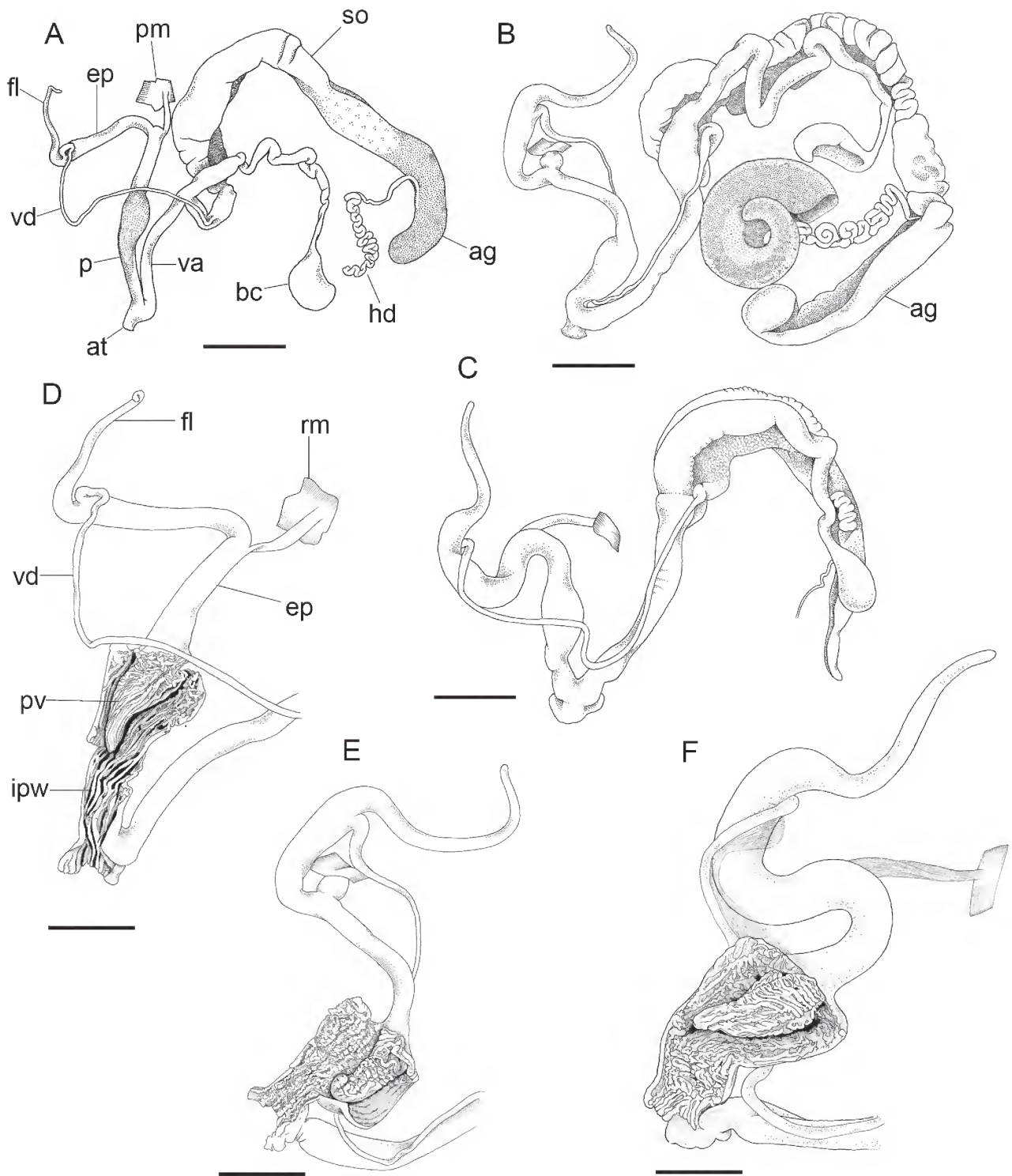


Figure 4. Reproductive anatomy of *Austrochloritis porteri*. (A–C) Drawings showing the entire reproductive system: (A) AM C.363835 (NSW, Upper Richmond River); (B) AM C.575455 (NSW, Mt Warning); (C) AM C.512605 (Queensland, Lamington NP). Scale bars = 5 mm. (D–F) Details of penial anatomy: (D) AM C.363835 (NSW, Upper Richmond River); (E) AM C.575455 (NSW, Mt Warning); (F) AM C.512605 (Queensland, Lamington NP). Scale bars = 3 mm. Abbreviations: ag—albumen gland; at—atrium; bc—bursa copulatrix; ep—epiphallus; fl—epiphallallic flagellum; hd—hermaphroditic duct; ipw—inner penial wall; p—penis; pm—penial retractor; pv—penial verge; va—vagina; vd—vas deferens.

Austrochloritis specularis Shea & Griffiths, 2010

Austrochloritis specularis Shea & Griffiths, 2010 (in Stanislav *et al.* 2010): 384, 536.

Material examined

Type material. Holotype QM MO27314 (from NE New South Wales, New England NP, Point Lookout region, 31°22'50"S 152°15'25"E [leg. D. & N. Potter, 8 Mar 1990, under logs]). Paratypes AM C.378010 (Gladstone SF, Reids Ck Rd at Moodys Ck crossing, 3.3 km from Kalang Rd, 30°28'52"S 152°50'21"E), AM C.339822 (Forest Way, 14.5 km SW Pt Lookout Rd, 30°34'23"S 152°14'24"E), AM C.339819 (Styx River, ca. 79 km E Armidale, nr Pt Lookout, 30°30'36"S 152°22'E).

Non-type material. NEW SOUTH WALES: New England NP, Point Lookout, 30°29'23"S 152°24'28"E (AM C.108470); Point Lookout, Platypus Valley Lookout track, 30°29'20"S 152°24'35"E (AM C.575464); New England NP, near Point Lookout, 30°29'36"S 152°24'23"E (AM C.108368); Oakes SF, Robinsons Knob Trail, nr Spring Ck, 30°33'S 152°28'23"E (AM C.337911); E of Armidale, W of Ebor, 6.6 km NW of Guy Fawkes intersection, Sandy Ck, 500m W of sand pit turnoff, 30°23'48"S 152°17'30"E (AM C.108452); E of Armidale, 750 m S of Lightning Knob, 30°30'55"S 152°10'44"E (AM C.108381); Cathedral Rock NP, northern boundary, 1 km W of Sandy Creek crossing, W of Ebor, Ebor-Guyra Rd, 30°23'35"S 152°16'33"E (AM C.575456); E of Armidale, E of Jeogla, 800m N of Forest Way on Jacks Fire Rd, 30°34'51"S 152°14'46"E (AM C.108365); Waterfall Way, 1 km S of junction with Guyra Road, W of Ebor, 30°26'31"S 152°18'58"E (AM C.561044); Oxley Wild Rivers NP, Youdales, 31°4'19"S 152°15'17"E (AM C.506320); Styx SF, Raspberry Rd, Halls Peak Rd crossing, 30°45'18"S 152°2'35"E (AM C.506286); 63 km ESE of Armidale, N of Raspberry Mt, 800m down Raspberry Rd, 30°37'17"S 152°10'30"E (AM C.339820); 63 km ESE Armidale, 15.2 km down Raspberry Rd, 30°40'47"S 152°08'E (AM C.339821).

Description

Shell (Fig 1D–E, Fig. 5). Medium sized ($D=12\text{--}16.5$ (average 14.3) mm, $H=8.5\text{--}12$ (average 10.0) mm, for $n=18$ lots), turbanate in shape with moderately raised spire, with on average 4.25 rounded whorls that weakly increase in diameter, sutures moderately impressed, protoconch sculpture of scattered pustules and rugose pustulose radial ridges, teleoconch sculpture of irregular growth lines with microsculpture of crowded pustules, periostracal sculpture of crowded curved setae, microsculpture of wavy periostracal ridgelets; end of last whorl descending below whorl plane, aperture moderately tilted from axis of coiling, with moderately thickened and reflected white to dark red-brown outer lip, columella slope about 45°; umbilicus narrow, partially covered by reflected columella, V-shaped in profile; shell colour from pale yellowish brown to dark reddish brown, with or without a narrow reddish brown spiral band around the whorl periphery.

External anatomy. Animal head-foot dark grey-brown; with retractable head at inner bases of ocular tentacles.

Reproductive anatomy (Fig. 6). Penis cylindrical, about as long as vagina, no penial sheath, inner penial wall with corrugated interlocking short longitudinal pilasters, distally giving rise to longitudinal rows of elongate strap-like pilasters; epiphallus cylindrical, about 3 times as long as penis, distal part with short epiphallic flagellum, epiphallus opening into penial lumen through narrow, pointed and finger-like, longitudinally grooved, penial verge, about half as long as penis, opening laterally; penial retractor attached

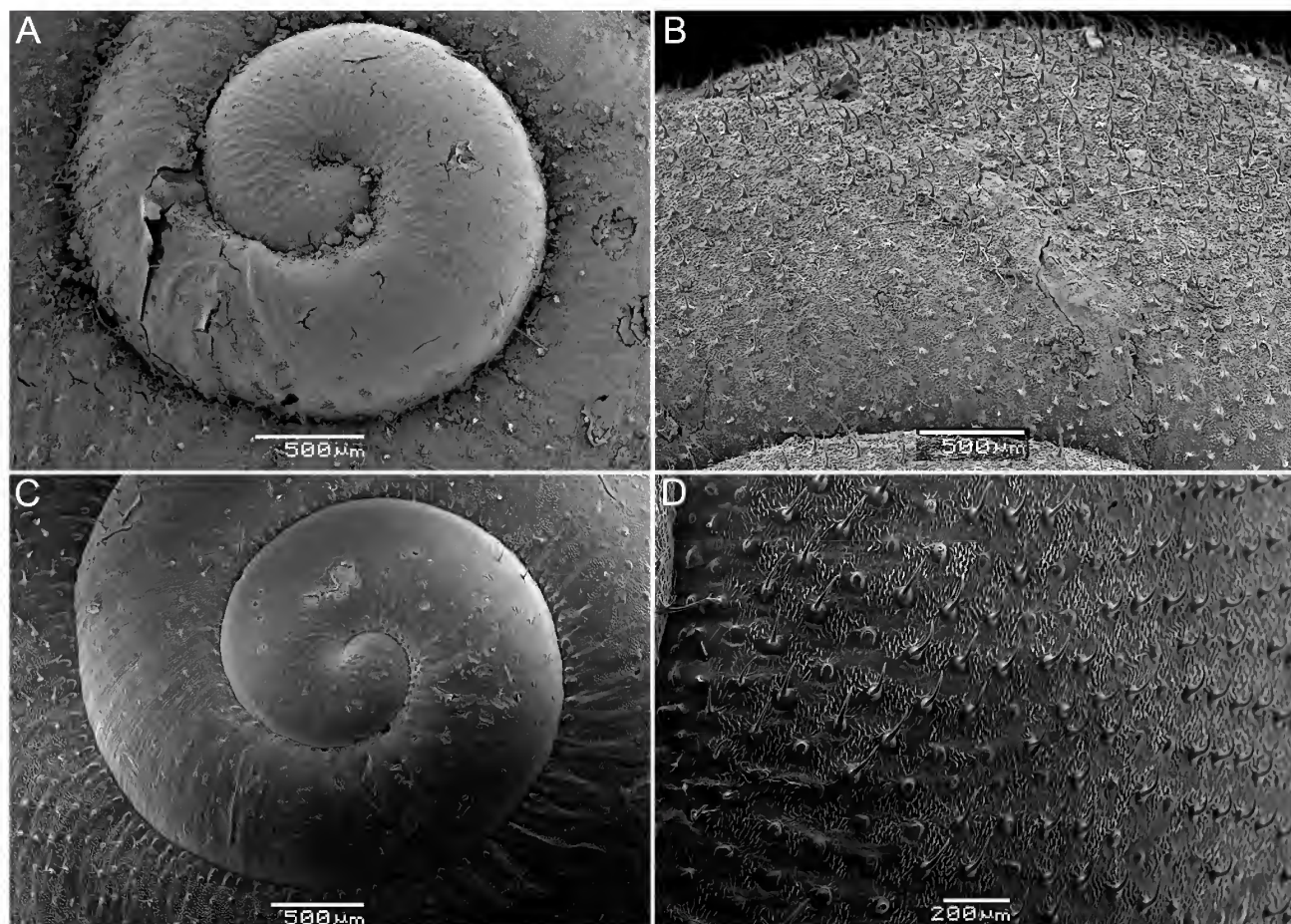


Figure 5. Scanning electron micrographs of shells of *Austrochloritis specularis* showing protoconch (left) and detail of teleoconch sculpture (right): (A–B) AM C.343464 (NSW, Ebor–Guyra Rd); (C–D) AM C.575456 (NSW, Ebor–Guyra Rd). Scale bars = 0.2 or 0.5 mm.

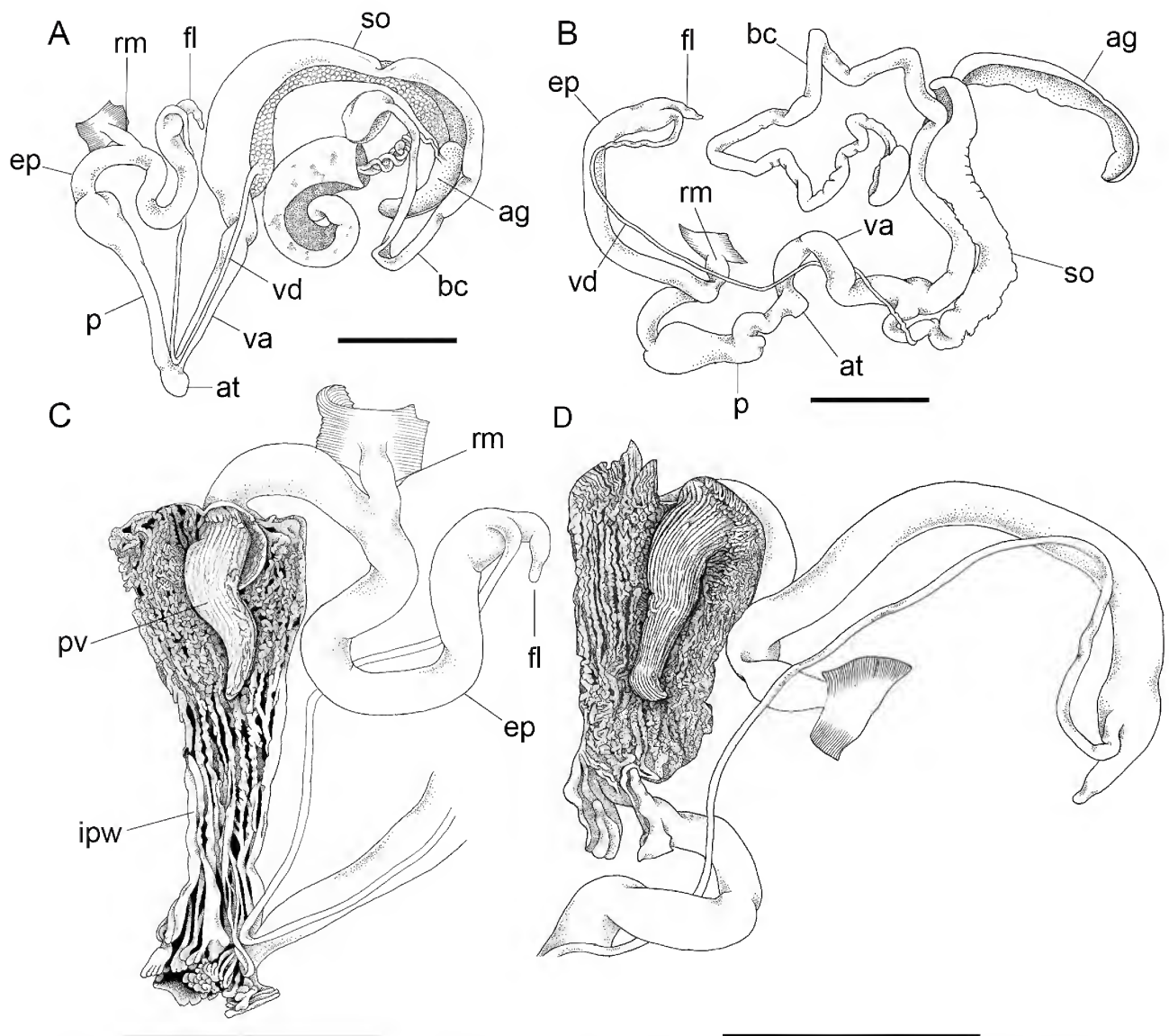


Figure 6. Reproductive anatomy of *Austrochloritis specularis*. (A–B) Drawings showing the entire reproductive system: (A) AM C.575464 (NSW, Point Lookout); (B) AM C.575456 (NSW, Ebor-Guyra Rd). (D–F) Details of penial anatomy: (C) AM C.575464 (NSW, Point Lookout); (D) AM C.575456 (NSW, Ebor-Guyra Rd). Scale bars = 5 mm. Abbreviations: ag—albumen gland; at—atrium; bc—bursa copulatrix; ep—epiphallus; fl—epiphallic flagellum; hd—hermaphroditic duct; ipw—inner penial wall; p—penis; pm—penial retractor; pv—penial verge; va—vagina; vd—vas deferens.

to proximal third of epiphallus; vas deferens entering head of epiphallus through a single pore just below base of epiphallic flagellum; vagina cylindrical, as long as penis, inner wall with very prominent longitudinal anastomosing pilasters, usually thickened around vaginal entrance; free oviduct short; bursa copulatrix long and thin and looped or folded several times, twice as long or more than oviduct length, with inflated bulb-like head, aligning with base of albumen gland; hermaphroditic duct inserting into head of talon.

Comparative remarks

Both species cannot be confidently distinguished by their shell, which is on average smaller in *A. specularis*, but exhibits very similar characteristics otherwise. However, both species differ in some reproductive characters, such as length of the bursa copulatrix relative to length of spermiduct (longer in *A. specularis*), relative length of

penis (about equal to vagina in *A. porteri*, but longer in *A. specularis*), length of epiphallus relative to penis (longer in *A. porteri*), position of the penial retractor muscle (at proximal third of epiphallus in *A. porteri*, mid-epiphallus in *A. specularis*), and relative length of the penial verge (half as long as penis in *A. porteri*), and the length of the epiphallic flagellum (much longer in *A. porteri*).

Distribution and ecology

Lives in dry to moist sclerophyll forests on the eastern edge of the New England Plateau and escarpment from Gladstone State Forest in the east to the upper Guy Fawkes River drainage north of Ebor and Point Lookout areas in the north to Youdales, Oxley Wild Rivers NP in the south (Fig. 2). Mainly found at altitudes over 900 meters on granitic or basaltic bedrock. Generally found under logs, rocks and shed bark around base of trees.

ACKNOWLEDGMENTS. This study has been funded by the Australian Government through an ABRS Bush Blitz Grant to FK (TTC216-16), which is gratefully acknowledged. Special thanks are due to Bruce Jenkins, Sydney, who donated additional funds to support this project. Thanks are also due to Sue Lindsay, Macquarie University, for producing SEM micrographs and to Des Beechey, Australian Museum, for specimen photography. The constructive comments of two reviewers, John Stanisic and Marco T. Neiber, helped to improve the quality of the final manuscript.

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The Flint Artefacts from two Workshops at Wadi el-Sheikh, Eastern Desert, Egypt

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ABSTRACT. A stone quarry at Wadi el-Sheikh is recognized as an important source of flint in ancient Egypt. In 1896–1897 a substantial sample of stone artefacts, from fifteen separate workshops, was collected and placed in various museums across the world. This material remains virtually unknown, including two assemblages kept in Australia, which are analyzed in this study. It is evidenced that both workshops produced predominantly flint knives and a smaller number of cleavers for distribution away from the quarry, in an earlier part of the third millennium Before the Common Era (BCE) often referred to as the Early Dynastic Period (c. 3150–2686 BCE) and Old Kingdom (c. 2686–2181 BCE). There is a strong indication that the workshops represent a tiny portion of a large supply network. Two types of tools, a pick and a hoe, are recognized as digging implements associated with a quarry, but are also present on sites in Egypt where excavation took place.

Introduction

Ancient Egypt is a prominent example of a highly-developed bronze-age civilization, later evolving into iron-age. It is often assumed that the refinement and splendour of Egyptian antiquity resulted, in large part, from the introduction of metallurgy, bronze smelting and casting that allowed production of specialized and highly effective tools—especially in contrast to the preceding stone-age period with more rudimentary technology and production capacity (Petrie, 1917; Barket & Yohe, 2011:30; Stevenson, 2011:74).

The use of copper tools and the evidence of small-scale smelting extends to the fourth millennium (and earlier), predating Dynastic Egypt of the third millennium BCE (Rothenberg *et al.*, 1998:4; Stevenson, 2011:650). Their presence and the production of sophisticated vases made of basalt, diorite and other hard stone material in the Nagada culture suggests that metallurgy indeed provided the foundation for Egyptian manufacturing capacity and

technical mastery (Bevan, 2007; Stevenson, 2011:65; Romer, 2012:104). Bronze tools, generally harder and more durable than copper, appeared in the Old Kingdom (Ogden, 2000:152). They were used and valued probably at the higher level of production associated with workshops servicing the royal court and high officials. However, stone tools, often made of flint, flaked in the manner familiar to humans for at least two million years, provided basic and essential hardware in daily life. Flaked stone tools were used in cutting, chopping, chiselling, carving, slicing and general processing of most of the organic and some non-organic materials, including fibre, reed, timber, bone, meat and hide—to name just a few (Kobusiewicz, 2006:459; Teeter, 2011:202; Graves-Brown, 2015; Lucarini, 2016:89–92). Such tools were used virtually throughout the entire ancient Egyptian history (Petrie, 1901b:80–81; Tillmann, 1994, 1999; Aston *et al.*, 2000; Graves-Brown, 2015; Barket & Yohe, 2011:30–31; Bard, 2007:73), showing that replacement of lithic technology by metallurgy took over 3000 years (Rosen, 1996:130).

Keywords: Wadi el-Sheikh; Ancient Egypt; technology; stone tools; knives; flint extraction; quarry

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Received: 27 February 2017 **Accepted:** 30 January 2019 **Published:** 24 July 2019 (in print and online simultaneously)

Publisher: The Australian Museum, Sydney, Australia (a statutory authority of, and principally funded by, the NSW State Government)

Citation: Florek, Stan, Thomas Hikade, and Sarah Carter. 2019. The flint artefacts from two workshops at Wadi el-Sheikh, Eastern Desert, Egypt. *Records of the Australian Museum* 71(4): 121–137. <https://doi.org/10.3853/j.2201-4349.71.2019.1681>

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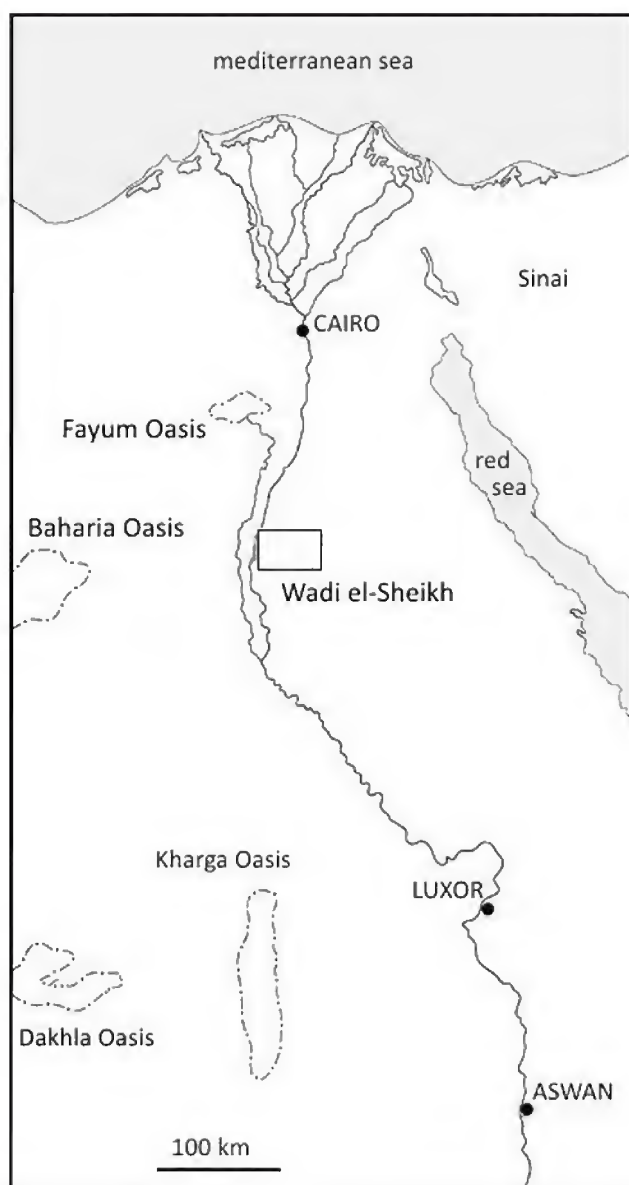


Figure 1. Location of Wadi el-Sheikh.

The great variety and richness of material culture, visual art and architecture, pictorial and written records of ancient Egypt attracted the attention of scholars and amateur enthusiasts of Egyptology from its beginning (Bard, 2007:8–15). Flaked flint tools were recognized and classified by Flinders Petrie (1902, 1903) at Abydos and in other works. But generally, an interest in flaked tools developed slowly in the last hundred years or so (Midant-Reynes, 1984; Weisgerber, 1987:166; Holmes, 1989:395–396; Svoboda, 1993; Bard, 2007:73). One of the episodes in this process dates to 1896–1897 when a prominent collector of “flints” Heywood Walter Seton-Karr (1859–1938) discovered (or rediscovered, to the benefit of Western scholars) and surveyed a complex of flint mining sites and workshops at Wadi el-Sheikh in the desert east of the Nile (Seton-Karr, 1898, 1905; Forbes, 1900; Baumgärtel, 1930).

The quarry complex is about 160 km south of Cairo (Fig. 1). The “mouth” of the Wadi is in relative proximity to the village of El Fant in the Beni Suef province. Seton-Karr estimates that from entering the Wadi at El Fant the quarry

complex extends about “30 miles” (c. 48 km) southeast from the River Nile (Seton-Karr, 1898:94)—it would be only half this distance in a straight line, east of Nazlet Awlad el-Sheikh.

During three weeks of fieldwork Seton-Karr surveyed and produced a relatively detailed map of the Wadi. He also collected 15 surface assemblages (estimated at over 500 kg of material) from separate and probably discrete stone workshops within the complex, all individually marked on his map. So far, we are unable to cross-reference individual assemblages with numbered locations on his map. Subsequently he donated or sold these assemblages to different museums in Europe, Egypt and even Australia (Weisgerber, 1987; Stevenson, 2013:80–81). One assemblage was sold to (what was then) the Mayer Museum in Liverpool (UK), together with documentation including maps and photos (Seton-Karr, 1898; Weisgerber, 1982; 1987:165).

In 1900 Henry Ogg Forbes, naturalist, ethnologist, and Director of the Museum of Liverpool published a relatively comprehensive article (Forbes, 1900), drawing on Seton-Karr’s documentation and artefacts in the collection. It appears Forbes (1900, 1901) did not have the same understanding of flint artefacts as Seton-Karr, but he recognized various flint tool categories and he even sourced the reproductions of rare Egyptian images, showing the manufacture of flint knives from tombs 2 and 15 of Beni Hasan, a necropolis in Middle Egypt, about 245 km south of Cairo (Newberry, 1893; Forbes, 1900:108–109; Lund, 2008, 2015; Teeter, 2011:202).

At about the same time, German geologist Max Blanckenhorn (Weisgerber, 1987:165) examined the mines of Wadi el-Sheikh and recognized the extent and importance of this complex. He also asserted a specific character of local flint that can be distinguished from other varieties of flint used in Egypt. The mines were examined again in the 1930s and 1960s (Baumgärtel, 1930, 1960); and more recently in the 1980s and 1990s (Weisgerber, 1982, 1987; Pawlik, 2000a,b, 2005).

However, it took a long time to truly recognize that Wadi el-Sheikh’s mines and related workshops are possibly some of the largest (Pawlik, 2000b, 2006) and maybe even oldest of this kind in Egypt. Recently a research team from the University of Vienna embarked on a study of Wadi el-Sheikh, conducting an extensive survey in 2014 (University of Vienna Middle Egypt Project: Wadi el-Sheikh. n.d.) and excavation (Köhler *et al.*, 2017; Klaunzer *et al.*, 2017).

As well as a more systematic investigation of the mines, the next logical step would be to examine the Wadi el-Sheikh flint tools—their supply and circulation throughout ancient Egypt, their geographical distribution, chronological framework, and the associated technical, economic and social factors (Barket & Yohe, 2011:30–31). For this to be successful, better identification and publication of flint tools in Egyptian settlements, villages and workshops would be required. It is encouraging to see that such investigations have been initiated (e.g., Holmes, 1989; Tillman, 1992, 1999; Pawlik, 2006; Kobusiewicz, 2006; Svoboda, 2006; Hikade, 2013).

This article aims to contribute to the growing body of evidence on the importance of the Wadi el-Sheikh mines in the Egyptian system of resources and provision of tools for daily work. It is based on small collections of flint artefacts from two separate workshops kept at the Australian Museum

(AM—about 130 artefacts, register numbers prefixed with *E*) and Museum Victoria (MV—about 120 artefacts, register numbers prefixed with *X*) which Seton-Karr donated in 1900. Some of the original Seton-Karr assemblages were not listed in previous ‘inventories’ and are not readily accessible. The Australian Museum’s collection is not mentioned in the previously published articles (Weisgerber, 1987:169–170).

We hope that the study of these two assemblages will contribute to a better understanding of the Wadi el-Sheikh mine-complex in Egyptian Pre- and Dynastic history. We are fully aware of the limitations of this study, where examination of spatial distribution within the site and even individual workshops, as well as direct determination of chronology, is virtually unavailable. But these assemblages provide an insight into flint tool production, distribution and some flint extraction methods deployed at Wadi el-Sheikh.

Assemblages from workshops

Studying flint material from Seton-Karr surface collections is difficult because what is usually taken for granted in normal archaeological practice (precise site location, its delineation, distribution of material within it), must be inferred from clues of variable reliability. From Seton-Karr’s reports (1898, 1905) and other published material (Forbes, 1900, 1901; Pawlik, 2000a) we understand that both assemblages were collected from relatively distinct, discrete production areas (compare Klaunzer *et al.*, 2017:9), not randomly from the wide background scatter. A few tool categories and their relative frequencies as well as numerous refits in both assemblages support this assertion. Moreover, they seem to represent small knapping areas or workshops of specific and discrete production episodes and generally not a superimposition of randomly accumulated material.

Seton-Karr, an experienced collector, must have recognized these factors in the field—as he marked on the map the areas from which his assemblages were taken. They were manageable for a small surveying party to describe and photograph and it was possible to collect entire or nearly entire knapped, surface material within them. It is unknown why Seton-Karr decided to collect only larger objects with complex patterns of flaking (leaving on site an entire subset of big and small flakes resulting from production), but it is entirely plausible he made a strategic decision to collect predominantly diagnostic and informative objects from many knapping areas instead of entire assemblages from fewer workshops—to use his short stay in the quarry in the most productive way.

In this section, we discuss the spatial and temporal integrity of material from the AM workshop in order to assess if and how the artefacts are related to each other. Such a step is essential for inferring to what degree the assemblage is a result of systematic human activity, contained in the small space and narrow time slot (e.g. measured in hours or days, not centuries or millennia). Our assemblages consist only of the flint artefacts selected and collected from the surface of a specific production area, of which the size and internal distribution pattern remain a matter of conjecture.

As mentioned the assemblage of flint artefacts at the Australian Museum (AM) consists of 130 pieces, while the Museum Victoria (MV) consists of 120 pieces (the exact number of artefacts is difficult to assess because some were

refitted before and some after registration. In addition, there are a small number of artefacts clearly or likely not related to ancient Egypt in both collections and these were excluded from this study¹). From reading Seton-Karr’s reports and consultation with Alfred Pawlik (pers. comm., 5 March 2015) we understand that items in each assemblage represent a selection from a far greater pool of artefacts discarded in the workshop. In selecting material, the collector probably used intuitive criteria, predominantly including size, complexity of flaking and general shape that could be interpreted as ‘intended.’ Such selection left the bulk of flint artefacts, especially flakes resulting from the reduction process, on site. In the archaeological analysis such flakes are informative; they would help to better understand the reduction processes, volume of production and support inferences related to finished, or partially completed, tools that were produced in the workshop.

Both assemblages contain only two categories of “products” (unfinished and/or broken): bifacially flaked stone knives (most frequent) and bifacially flaked cleavers (the use of this term is discussed later in Classification). Two other distinct forms, picks and hoes seem to be associated mostly with digging and flint extraction. Such content indicates that both workshops were narrowly focused on production of knives and some quantity of cleavers and therefore were task-oriented, discrete entities of short duration.

It is significant that not a single artefact visibly made from a flake or blade is present in our assemblages.² Every artefact is made (as far as it is possible to detect) by the bi-facial flaking of a larger and elongated flint block or tabular piece until it was shaped into the intended form, and mostly discarded when it broke (Fig. 2). Complete final products were, of course, carried away (Köhler *et al.*, 2017). Broken flints show that typically any piece shorter than 18 cm was discarded (with a few exceptions). This provides the first general approximation and some insight into the manufacturing process that took place in the workshops.

Refits

In the AM collection 30 artefacts (23%) are fragments (halves) that, when refitted, made 15 complete or nearly complete artefacts, predominantly knives (5, Figs 3–5) and knife preforms (possibly 5, Figs 4, 6). The remaining five are cleavers (Figs 2, 13) and possibly one crescent knife (a form infrequent in our assemblages, Fig. 9). This relatively high number of refits casts light on the integrity of the assemblage from the workshop, its spatial organization and ultimately the nature of the production process.

Seton-Karr made his collection of artefacts from 15 workshops in a relatively short time—three weeks including a cartographic survey (Seton-Karr, 1898). If he applied his collection criteria consistently he would probably have collected entire subsets of artefacts from each workshop—all recognizable larger forms with complex flaking—and this would be practically possible when workshops were contained within several square metres, not hundreds or thousands of square metres.

If broken pieces, from the same intended product, were discarded far apart or moved apart later, they would be less likely to be collected in the same assemblage. The high number of refits suggests that the workshops were small with

a high density of discarded flints (Forbes, 1900:104, second photo; Pawlik, 2006:207–208, figs 28, 30; Klaunzer *et al.*, 2017:9, fig. 7). This in turn would imply that workshops resulted from production by one or a few people, working consistently in probably one or a succession of flaking episodes in a day or several days—returning to the same spot for logistical reasons such as availability of suitable flint, tools brought and left on the ground, possibly some setup such as provisional shelter, water and food supplies stored nearby (Weisgerber, 1982:202–203; Negro & Cammelli, 2010:115; Klaunzer *et al.*, 2017:8). The labour cost of finding and establishing a reasonable extraction and production area would present an incentive to exploit it for as long as it provided good return without increasing the labour-cost of production.

Experimental knapping in general (performed by Florek) indicates that the flaking process is normally fast, and an experienced artisan would be able to produce a significant number of tools in several hours, as long as the supply of flint, knapping tools and some degree of work comfort were provided. One of the authors (Florek) observed broadly similar workshops in the silcrete quarry near Lake Eyre in South Australia, where stone blade-knives were produced in large numbers. Knapping workshops with high density of artefacts (flakes, preforms and discarded pieces) were located near the spot of stone extraction (shallow digging in a silcrete outcrop) and were essentially contained within an area of about 4 m in diameter (less than 12 m²).

If broken halves were tossed aside they would still be only a few metres apart, if not they would be discarded and left virtually side by side.

Desert varnish

Desert varnish is a dark coating often found on rocks after long exposure in desert regions and its colour, which varies from shades of brown and red to black, results from a chemical process involving iron and manganese oxides (Perry *et al.*, 2015). The formation of desert varnish is believed to be slow, measured in millennia (2,000 years is often quoted), but it has been observed to develop much faster, suggesting that it is dependent on specific local conditions.

Such varnish, or dark patina, is a distinctive feature of flint artefacts at Wadi el Sheikh, attesting to their long exposure to desert conditions on the ground surface (Köhler *et al.*, 2017).

Desert varnish observed on the specimens from the AM workshop assemblage tends to be present only on one side of the artefacts. Most of the flints have a definite varnish on one side while the other side remains relatively “fresh”—signified by a light creamy-grey colour. In some cases, such as broken knives, varnish is on different sides of each half (Figs 3–5). This pattern suggests a relatively low level of disturbance after initial flaking took place and broken pieces were discarded. While this observation is not quantified it provides a good indication that our workshop resulted from a single or a few episodes of production closely linked in time and probably by the same person or persons, rather than being a deposit of separate production episodes unrelated to each other and far apart in time.

General pattern

The overall pattern of artefacts, their form, relative frequencies, refits, distribution (inferred) and desert varnish implies a reasonable level of integrity of the assemblage (with a few ‘foreign’ intrusions). This permits us to draw some tentative conclusions. In the light of such evidence it is possible to imagine that the AM workshop was used within the quarry complex as a short, possibly for one or a few days, production area where one or a few artisans from the same (?) expedition-group worked to make a sizable supply of knives, and probably some other tools. It would be interesting to assess how other assemblages collected by Seton-Karr compare to our two collections, and if there is any spatial or temporal link that could be detected between them.

The two assemblages from Wadi el-Sheikh examined for this study, AM and MV, show noticeable similarities, especially in the form of flint artefacts, their relative frequencies, refits and desert varnish. Some of these characteristics were observed systematically only for the AM collection. The MV collection provides a good comparison for classification, size of artefacts and their relative frequencies. The Museum of Liverpool collection is most useful for typological comparison, but it is difficult to extract quantified data from the report (Forbes, 1900).

Chronology

The size and extent of the Wadi el-Sheikh quarries suggest they were used as a source of flint tools for millennia (Pawlik, 2006; Köhler *et al.*, 2017; Klaunzer *et al.*, 2017)—perhaps in two phases of greater intensity in the 3rd and 2nd millennium BCE respectively as suggested by Hikade (2013:25). Mining shafts have been estimated to date to about 3,300–2,800 BCE, but used more extensively during the Middle Kingdom (Mangum, *n.d.*; Negro & Cammelli, 2010). It is conceivable that numerous extraction and production areas, such as our workshops, could collectively cover a period of a few millennia. Yet, as we asserted earlier, a workshop would result from very short and discrete activity anywhere in the chronological duration of the quarry. The assemblages in this study cannot be directly dated, but can be attributed to a broad chronological period on a basis of the diagnostic artefacts—predominantly stone knives. In general, the knives of this type appeared in the Predynastic Period, were most frequent in the Middle Period and persisted until the New Kingdom, to about the middle of the 2nd millennium BC (Svoboda, 2006:505–506; Kobusiewicz, 2006:455; Graves-Brown, 2010:533–540; Graves-Brown, 2015:21–22). They did not disappear completely but possibly were partially supplemented or replaced by bronze tools (Kobusiewicz, 2006:455; Graves-Brown, 2015:21–22). These types of knives, known from other dated archaeological sites in Egypt, such as Abusir, Giza, Tell Ibrahim Awad, Kom al-Ahmar, Elephantine, and some sites at the oasis such as Dakhla show an association with the Early Dynastic Period and the Old Kingdom (Svoboda 1993, 2006; Kobusiewicz, 2006; Pavlik, 2006; Graves-Brown, 2010; Hikade, 2013). Cleavers and picks (as we call them, including the adze or hoe and pick³ as designated by Graves-Brown, 2010:561–565), are also mostly associated with the 3rd millennium BCE.

A similar conclusion is drawn by Pawlik (2006) and more recently by Hikade (2013) based on the analysis of archaeological sites Kom al-Ahmar and Elephantine respectively. In addition, both authors evaluate Wadi el-Sheikh in light of published material, identification of flint and some limited inspection of the site, indicating that the early phase⁴ of the quarry relates to Early Dynastic and Old Kingdom periods (Hikade, 2013:24–25; Köhler *et al.*, 2017:13–14; Klaunzer *et al.*, 2017:5).

Both our assemblages are likely associated with 3rd millennium BCE. By sharing the same characteristics (e.g., focus on bifacially flaked knives, an apparent lack of blade artefacts, comparable relative frequency of tool categories) they appear as replication of a similar process of tool provision and therefore could represent a broader system of supply.

Classification

When analyzing the two collections (AM and MV) we realized that most artefacts we encountered, both tools and preforms, are not well documented and recognized in the literature. Some researchers are familiar with the types we encountered in these assemblages (Setton-Karr, 1898; Petrie, 1902; Forbes, 1900; Tillmann, 1992, 1994; Graves-Brown, 2010; Svoboda, 2006; Kobusiewicz, 2006; Pawlik, 2006; Hikade, 2013; Köhler *et al.*, 2017), but for some types there is no consistent classificatory framework, systematic interpretation or reliable reference (compare Holmes, 1989:395).

We recognize four major product categories: thin elongated knife (Figs 3–5), flat elongated cleaver (rectangular or triangular, Figs 12–13), thick elongated pick (Figs 15–16), and hoe or hoe-like tool (Fig. 17). We infer, and will discuss further, if and how these four tool types were systematically associated with the workshops.

Furthermore, we recognize three categories of preforms: early blank, second-stage (middle) preform and advanced preform, the last being close to the finished product (cleaver—Figs 12, 13; knife—Figs 3, 5; or pick—Fig. 14).

Table 1. Artefact categories for AM and MV.

	AM	%	MV	%
blank early	4	3.4	1	0.8
blank middle	10	8.6	2	1.7
cleaver	14	12	26	22
pick	8	6.9	25	21.2
hoe	4	3.4	5	4.2
knife complete	5	4.3	1	0.8
knife fragment	48	41.4	47	39.8
knife blank	8	6.9	7	5.9
knife crescent	7	6	3	2.5
double sided biface	4	3.4	1	0.8
unclassified	4	3.4	—	—
total	116	99.7	118	99.7

Blanks

Early blanks range from just under one kilogram to nearly 1.5 kg. They are elongated, thick, bifacially flaked forms. It is difficult to infer into what implement they were intended to be made. There are only four such blanks in the AM collection (two unbroken) and one in the MV collection. It is not clear why they were discarded and why so few are present.

Early blanks could have been abandoned because of a lesser than expected flaking quality of flint or the artisans were testing a number of flint nodules brought to the workshop without any intention to turn them into an actual tool. It could be that workers ran out of time or incentive to complete a particular task. A combination of these factors may be taken into account. The relative rarity of early blanks may also be explained by the fact that they are less likely to break, and therefore are usually developed into a more advanced stage or actual finished tool. Finally, it is difficult to know if the collector selected a small sample of early (heavy) blanks for logistic reasons, while collecting in more systematic manner lighter, advanced forms.

Early blanks provide an insight into the ‘typical’ reduction process, which involved large elongated pieces of flint flaked bi-facially. All flaked tools associated with workshops were elongated, while cleavers and knives were also thin. For a complete knife an artisan would have flaked off well over one kilogram of material and over half a kilogram for an average cleaver. The workshop would contain a large volume of waste flakes resulting from the reduction process (Hikade, 2013:25; Köhler *et al.*, 2017:30). This also provides evidence for a basic reason for which production took place at the quarry—transporting early blanks out of the quarry would be an extremely inefficient strategy, consuming and wasting a lot of energy and effort.

Second-stage blanks (12) are significantly lighter (379 g on average—including halves and fragments) and thinner pieces (up to 2.4 cm). Some are still too general and could be potentially made into either cleaver or knife. Other blanks show the relatively clear characteristic of a preform for either a cleaver or a knife. A cleaver preform tends to be rectangular or, more commonly, triangular and thicker (up to 2.7 cm); a knife preform tends to be narrower and pointed at both ends, curved on one side and nearly straight on the other, and is generally thinner (up to 1.5 cm).

The comparable pick preform, at this stage of production, is thick and usually distinctive enough to be classified as an incomplete tool, where only minimal flaking, by volume, is required to give it a final shape (Fig. 14).

It proved impractical to separate advanced preforms from nearly finished tools. Although some knife or cleaver fragments have well developed edges and fully worked surfaces, others need more thinning and the surface shows a substantial amount of cortex. In essence all broken pieces are unfinished or almost finished products and can be considered advanced preforms. Several knife fragments (especially so in the MV collection) were made of thin pieces of tabular flint (compare Lucarini, 2016:89; Klaunzer *et al.*, 2017:16), meaning they were already very thin and light while the edges needed to be fully formed and a good amount of cortex remained, sometimes on both sides. This shows that some economizing strategy was deployed, where numerous knives were not made from large early blanks but flat pieces which required far less reduction, although they were potentially more prone to breakage.

Table 2. Complete (refitted) knives (Australian Museum).

collection	length	width	thickness	weight
numbers				
E9681	23	6.5	1.2	222
E9688	26	7	1.6	248
E9616	21	8	1.6	332
E9617	19	6.5	1.2	170
E9595	24	10	1.5	450
X6846	22	8	1.8	311
average	22.5	7.7	1.5	289

Knives

Six “complete” knives (refitted/reconstructed from two pieces) illustrate that, with slight variation, they conform to a broader form dated to the 3rd millennium BCE (Kobusiewicz, 2006; Graves-Brown, 2010; Hikade, 2013). The knives are quite thin (c. 1.5 cm on average), elongated (c. 22.5 cm on average) and broad (c. 7.7 cm on average—compare Svoboda, 2006:505). The knives weigh 289 g on average, ranging from 170–450 g. There are five knives in the AM collection (prefix E) and one in the MV collection (prefix X). The knife from the MV collection is close to average in size and weight, but slightly thicker.

These knives tend to be broader and pointier at the distal end and narrower and less pointy at the proximal end (Graves-Brown, 2010:538–539; types 3, 7, 8). The smallest knife (E9617) and one advance preform (E9614) have an overall shape resembling a spearhead, with the upper edge curved nearly as much as the lower (Fig. 3), but a visible asymmetry and size allows them to be classified as knives.

Knife fragments (halves) comprise 65 artefacts (56% of the total) in the AM collection, and 52 (44%) in the MV collection. They are, on average, almost exactly half the length (11.5 cm) of the complete knives (22.5 cm). The quantity of knives and their fragments strongly indicates that knives were the main object of production in both areas represented by the AM and MV collections.

Furthermore, we identified 8 (6.9%) knife blanks (or preforms), in the AM collection and 7 (5.9%) in the MV collection. In different stages of reduction, they illustrate an intermediate stage of knife manufacture (Figs 4–6). Such preforms underwent bifacial reduction, aiming to form quite thin, elongated forms, slightly pointed at both ends, and reasonably broad until they broke. Complete knives were undoubtedly carried away from the quarry. We believe early blanks (c. 650–880 g) were less likely to break and hence the relative scarcity of such blanks in both assemblages. Conversely, the blanks (and their fragments) in the advance stage of reduction (c. 130–340 g) are more numerous and are

usually significantly thinner and lighter. Six such blanks in the AM collection are longer than 18 cm but only 2 of them are unbroken (others are made of two parts).

Most of the knife fragments appear similar to the complete (reconstructed) knives (Graves-Brown’s types 3, 7, 8; also Svoboda, 2006:505–506; Pawlik, 2006:198, fig. 8 and p. 200, fig. 16). They appear relatively straight (or nearly straight) on one edge and curved (to different degree) on the other edge, as well as a variously pointed or slightly rounded end (Figs 7–8). A few fragments are so broad and curved at one edge (Fig. 11) that they may represent what we call a crescent knife (Graves-Brown, 2010:543; type 1). Few artefacts in the AM collection may be interpreted as preforms of crescent knife (Fig. 9).

Some knife fragments are finely crafted, suggesting workshop production was not to provide nearly complete tools but rather fully finished products, ready for distribution and use. This assertion is supported by a finishing touch detected on a few knife fragments. Bifacial flaking of thin pointed forms would encounter an acute technical problem at the pointy end. Even light pressure or tapping would likely break the narrow tip. So, to prevent this from happening, the last tiny flake was removed not from the edge (in a right angle direction to the edge) but from the tip in the longitudinal direction, thus creating what technically looks like a micro-burinated tip. It is worth noting that such a technique was used in the production of Middle Palaeolithic points of southern African industries (e.g., Still Bay—Soriano *et al.*, 2015, fig. 9.7), reinforcing the view that Egyptian flint artisans inherited and adapted a very old technical tradition of superbly mastered craftsmanship. This also validates our understanding that the Egyptian civilization emerged from African roots with some technical and cultural preconditions embedded in a long human history, bridged via the Neolithic progress (Kobusiewicz, 2006:449; Brionis *et al.*, 2012:188–189; Wengrow *et al.*, 2014; Stevenson, 2016; Lucarini, 2016:96).

We observed that some knife fragments were further modified (e.g., E9627 Fig. 10), as though an attempt was made to reshape them into smaller, nearly complete knives, or simply any functional knife. These partially repaired and discarded knives suggest that ultimately, they were considered unacceptable. They also suggest that, possibly, some larger fragments, such as longer sections of broken knives, were successfully re-modelled and taken away from the quarry. This may explain, at least partially, why flint assemblages not from quarry sites, often contain knives that vary in form and size (e.g., Svoboda, 2006; Graves-Brown, 2010; Pawlik, 2000b:5; Lucarini, 2016:88).

It is possible that tanged knives represent an early stage of further modification (adjustment) through use, which would continue via re-sharpening and ultimately result in their disappearance as recognizable tool form (e.g., Svoboda, 2006:504–506).

Our identification, with 73 (63%) of all artefacts in the AM collection directly associated with knife production; and 59 (50%) of all artefacts in the MV collection, provides good insight as to the main purpose of flint reduction in both workshops. However, 24% of artefacts in the AM collection and 50% in the MV collection represent three other tool categories, cleaver, pick and hoe.

Table 3. Knife fragments, including preforms.

	total	knives	%
Australian Museum	116	73	63
Museum Victoria	118	59	50

Cleavers

Flat and mostly trapezoid/triangular forms we call cleavers are known under a variety of terms—mainly implying their function—such as axe, plane, hoe and chisel.⁵ Our preferred term, cleaver, implies that it is not an imitation of metal Bronze-age tool or even Neolithic axe but a flaked tool with an old ancestry (Paleolithic) and its own specific characteristic in manufacture, use and re-sharpening.

Cleavers and their preforms account for 14 (12%) pieces in the AM collection and 26 (22%) in the MV collection. They are flat, tabular, elongated forms; some are rectangular, but most are triangular (or trapezoid/triangular), broadly similar to forms illustrated in Forbes (1900: figs 9–17), Petrie (1902: plate XX) and Pawlik (2006:202, figs 18–21). There are a few cleavers neatly shaped (in a technical sense) while many are not fully formed or complete. Such a distinction may not be significant as most cleavers with a sharp cutting edge are effective tools (we consider the cutting edge to be the broad end of an elongated triangle; the narrow, pointed or round end would be equivalent to a handle). A cleaver with a developed working edge is a fully functional tool, regardless of how much and how finely or crudely its other edges are formed or how much its surface is worked over. Several cleavers have a slightly curved cutting edge (Fig. 12). Like knives, they would be re sharpened during use, gradually becoming shorter, lighter and less recognizable as morphologically distinctive tools.

The cleavers in our assemblages, characterized by bifacial flaking, are, on average, 16.5 cm long, 10 cm wide, nearly 2.7 cm thick (range including preforms: 1.7–4.5 cm). Generally the straight cutting edge, calculated for 40 cleavers, is nearly 9.8 cm wide on average (range: 8.0–11.5 cm). The average weight is close to half a kilogram (484 g). Cleavers in the AM collection are slightly longer, wider, thicker and heavier (AM: 563 g, MV: 406 g).

Picks

Picks and their preforms comprise 8 (6.8%) pieces in the AM collection and 25 (21.2%) in the MV collection. It would appear that picks were often made from coarser, less glossy flint, or perhaps silicified limestone (Köhler *et al.*, 2017:18) which probably would be compatible with tools designated for robust work where more force than fine cutting was required.

A pick is an elongated tool with a broad and thick body and distinct knob-like handle formed at one (proximal) end (Forbes, 1900, fig. 37; Köhler *et al.*, 2017, fig. 10)⁶. A narrow chisel-like working edge is formed at the distal end by flaking back from the dorsal to the ventral side to produce a chisel-type edge, with a steep or low angle (Figs 15–16). The body has a distinctly flat dorsal side while its ventral side can be flat (rectangular-trapezoid cross section Figs 15–16) or with a crest (triangular cross section Fig. 14). Most such picks in the AM collection are flat on the ventral side. Forms with a crest are predominantly in the MV collection.

It is tempting to assert that picks were used for mining flint in the quarry (Weisgerber, 1987:169; Köhler *et al.*, 2017:12). A chisel-like cutting edge would be suitable to penetrate the soil and break through an eroding limestone layer of desert surface and subsurface deposits. “Mr. Seton-Karr has suggested that these ‘truncheons’, as he names them, were tools used at mines by the artificers ... in the fabrication of

other stone implements, or to dig the flint nodules out of the limestone in which they occur.” (Forbes, 1900:99). Longer picks with a more acute cutting edge (low angle between dorsal and ventral surface e.g., less than 40°) may be closer to the original form which, through use, would be transformed to shorter picks with a steep cutting edge (close to 80°) often looking battered and irregular. The AM collection picks are consistently close to 20 cm in length and, apart from one unfinished piece, have longer, more protruding cutting edges. The MV picks show more variation in size, but one third are shorter than 19 cm and many have a short, battered, steep cutting edge. If the variation of picks between the AM and MV collections can be interpreted (despite being a small sample), it is possible that in the first workshop they were mostly manufactured and used less intensely, while in the second workshop they could be manufactured and used more heavily—for digging on the spot or very near—hence shortened through use.

Hoes

Four pieces in the AM collection and five in the MV collection resemble hoe-head tools (Forbes, 1900, fig. 42). The body is generally shorter than that of a pick (by 5 cm), as well as being narrower and nearly pointed at the proximal end. The working edge is broad and with flaking back onto the ventral side it resembles a platform of a core with an extremely low angle (Fig. 17). In a very broad sense it is similar to a cone with an extremely slanted platform (stone tool specialists may be justified in calling it a core). The form of the proximal end, especially compared to a pick, suggests that these hoe-like tools may have been fitted with a handle.

It is possible that this tool of wedge-like form was used for digging or scraping soil or rocky detritus, where its broad working edge (core’s platform) would be used as the hoeing “end”, penetrating less compact loam and scooping it towards a digger.

We conceive that the flint “hoe” may not have been suitable for prolonged use and hence not expected in an agricultural context, but it was easy to make where the supply of flint was plentiful and to attach an impromptu handle if necessary.

Picks and flint “hoes” combined could be considered sufficient mining tools to break compact loam and remove smaller detritus from the pit or shaft. We hope future research will help to clarify or modify this assertion.

Discussion

The analysis of two small assemblages of flint conducted in this study is insufficient to draw any broad inferences about the Wadi el-Sheikh Quarry complex, but it helps to confirm, in a systematic manner, its use for the provision of daily tools in the 3rd millennium BCE. And it helps to confirm that the tools produced in two analyzed workshops were predominantly flint knives. Such knives, of various types, may not be as common in the archaeological deposits of ancient Egyptian settlements (e.g., Kobusiewicz, 2006; Hikade, 2013), because their numbers would rapidly deplete through use, re-sharpening and recycling (Svoboda, 2006; Lund, 2008). The quarry site provides a different perspective of the use of knives and their supply and demand. Our study is not designed to quantify such matters in a wide

geographical and chronological context. But if the knives were used in a similar way, for a great variety of tasks in everyday life (e.g., Ikram, 2000), as better documented with metal knives in Roman and Medieval times, for instance, we would have to consider a massive collective demand (compare Kobusiewicz, 2006:459). And yet, via a recycling process, flint knives would whittle away, in a metaphorical and actual sense (Svoboda, 2006), in Egyptian households and workshops, where they would appear as a numerically minor component of daily utensils.

Our two assemblages cast light on the supply of flint tools, but some assumptions and hypothetical estimates are necessary. How many tools did each workshop produce? Broken knives and cleavers left on the ground provide us with important clues. It is likely that broken fragments represent relatively regular production errors, whereby every flaking session would result in a portion of broken preforms and nearly complete products. For example, if for every 100 knives attempted or completed, 25 were broken, we could infer they indicate 75 completed knives produced and taken away from a workshop. While true that the percentage of error is variable and unknown, we intend to provide only an indicative volume of production to illustrate the role of workshops in a provisioning system rather than to quantify the system itself.

If we assume, for example, a very high production error (breakage) of 25%, the AM workshop would have supplied 219 knives and MV 177 knives. With a lower, and probably more realistic, breakage rate of 10%, AM would have supplied approximately 657 (c. 190 kg) knives and MV 531 (c. 153 kg) knives.

For an illustrative purpose alone⁷, if all 15 assemblages collected by Seton-Karr produced a comparable number of knives (594, c. 172 kg each on average), collectively they would supply 8,910 knives of a total weight of almost 2.6 tonnes. All this could have been supplied by a team of two or three artisans and two donkeys going to the quarry every third week of the year for about three to five days each time. Ten such teams, not an unrealistic assumption, would produce 89,100 knives (about 25.7 tonnes) annually. We suggest that while individual workshops reflect only a short production episode, collectively they could represent a significantly large network for the production and distribution of knives in the region (Barkett & Yohe, 2011:27).

If the procurement of flint knives was indeed organized in such or a similar manner it would be consistent with our assertion that finished knives, rather than blanks, were produced and transported out of the quarry (compare Pawlik, 2006:196–198), because any excess of weight would compound the logistics of transport and distribution. There is also compelling evidence that pack-animals in Egypt were typically overloaded with excessive burdens (Rossel *et al.*, 2008:3719).

We believe that the small, compact and focused character of the workshops, combined with a general knowledge of the environmental quality of the Eastern Desert, permits us to broadly infer both the human involvement and duration of work performed. Environmental constraints would induce a working team to be small and operate for a short period of time. In normal, usually arid conditions, food and water for people and pack animals would be brought to the mining complex (Köhler *et al.*, 2017:30). At least half

a day's journey each way (approximately 20–30 km) and two days of effective flint extraction and manufacturing of stone tools would require a sizable quantity, in volume and weight, of water alone. On the other hand, we estimate two artisans could produce close to 600 flint knives in two days—close to the load limit of around 170 kg, for two donkeys. Thus, our hypothesis is that each of our workshops could reflect an expedition of two artisans with two donkeys for a total period of three days (a similar estimate was made independently in Köhler *et al.* 2017:32–33). It is possible that we underestimate or overestimate the speed and efficiency of the production, but we feel that in general our calculation is realistic. It is also possible that these expeditions were larger and that they would result in many workshops similar to those included in this study. However, we believe each workshop of comparable size would translate to roughly 3 days, 2 people and 2 animals, operating as an autonomous unit or as part of a larger group.

The same logistic concern for transporting a large volume of products from the quarry would justify our hypothesis about the “mining tools”. We believe that picks and hoes are tools associated specifically with the quarry and with construction sites where excavation into bedrock was required, on which we comment below.

The mining tools were made and used within the quarry and, to our knowledge, rarely occur in typical domestic (village or urban) sites, or in temple and sepulchral contexts⁸. These heavy-duty and heavy tools (picks weigh around 636 g on average, but there are some close to and over 1 kg) were probably made, used and discarded within the quarry as the plentiful supply of flint did not offer any incentive for their curation, i.e. they were readily made when needed and also readily discarded.

We observed that the pick tools generally appear in a more advanced state of use in the MV assemblage (where they are more numerous) and in a less advanced stage of use in the AM assemblage, where some pick blanks and at least one “freshly” made tool are present. Such variation invites the question: were picks also produced for use beyond the quarry and transported out of it for distribution? Our material does not permit us to address this directly with supportive evidence. We can only hypothesize that picks were produced in smaller quantities because, compared with knives, they were more specialized tools and, being heavy, rigorously selected for transport. What was left in the workshops were used picks with battered cutting edges and complete specimens which were considered less worthy and/or unnecessary to transport. We believe that for specific construction projects (e.g., tomb or temple), special system of provisioning of “mining tools” was required (discussed briefly in Köhler *et al.*, 2017:5–6) and workshops where such tools were made may be discovered in the Wadi el-Sheikh Quarry complex and in other quarries.

Seton-Karr (1905) recognized a pick tool used for excavation at Thebes and he links this to his previous observation of such tools at Wadi el-Sheikh Quarry. Other researchers also recognized pick tools in graves (Armant, south of Thebes) where it can be interpreted as associated with digging (Myers & Fairman, 1931:224).

One tool that may have been rare, and probably carried by the craftsmen, was a hammer-stone. Only one such tool (from Seton-Karr collections) is known to date, and is illustrated in the report from the Museum of Liverpool collection (Forbes,

1900:93; figs 39–40). It is possible that a hammer-stone of sufficient quality (though probably basaltic “spherical” rock) would be brought to the quarry and valued for its rarity and essential service. We hypothesize that a hammer-stone in serviceable form would rarely be discarded. However, it must also be considered that such a tool would be less likely recognized as an artefact and more easily overlooked by casual or amateur collectors.

If the same breakage ratio (10%) is assumed for the cleaver, the AM workshop would supply 150 cleavers (84.4 kg), and the MV workshop 260 cleavers (105.5 kg). For the same illustrative purpose, all 15 workshops would supply approximately 3,075 cleavers (1,490 kg). A cleaver is a heavy-duty chopping tool used for working wood, bone and relatively soft rock such as limestone. Unlike a pick it is a more universal tool, expected to be present in ordinary domestic sites as well as in special workshops (Hikade, 2013). In addition, a cleaver would be associated with masonry sites where blocks or plates of limestone or sandstone were manufactured. Indeed, cleavers appear more frequently in archaeological sites throughout Egypt (e.g., Petrie, 1901a). This tool would also be re-sharpened and possibly recycled.

Conclusions

Our study of two flint assemblages from Wadi el-Sheikh illustrates that metal tools augmented rather than replaced stone tools and related technology in the 3rd millennium and even earlier in Egypt (Hikade, 1910:8–9). We know from other sources that this parallel use of stone and metal technology continued through nearly the entire history of ancient Egypt (Graves-Brown, 2015; Barket & Yohe, 2011:30–31).

The kind of tools prevalent in the workshops strongly suggests that flint knives were produced in quite a standardized and focused manner for distribution and use away from the quarry. A few examples of short knives, probably remade from broken fragments, and crescent knives indicate a degree of opportunism in fulfilling production quotas by economizing on time and labour invested at the quarry.

The form and quality of broken pieces left in the workshops indicate that knives were more likely produced in their final stage, ready for use, rather than as preforms to be completed beyond the quarry. The reason for this was

probably a need to economize the logistics of transport, which in turn was dictated by the sizable volume and weight of knives manufactured in the workshops. We estimate each small workshop, active for a period between one and three days, would supply several hundred knives—an average load of about 170 kg.

Both workshops produced a smaller number of cleavers for distribution and use beyond the quarry. The nature of the evidence makes it more difficult to demonstrate in which state of completeness these tools would be transported from the quarry. But it is reasonable to expect that the same logistical need for economizing on the transport load that we observed with knives would apply to cleavers. As heavy-duty tools, the need for fine-finished cleavers was probably less important, but it would be motivated mainly by the imperative to reduce the overall volume of each tool to its optimal weight. However, broken fragments of cleavers left in the workshops show few examples of well-finished tools.

Our study confirms that the pick was a digging tool, predominantly associated with construction and mining sites. A sizable collection of picks (33) from two workshops permits us to draw some inferences about their typology, manufacture and use. The context suggests picks combined some of the qualities of a pick and chisel, capable of digging compact soil as well as soft rock such as lime and sandstone.

Nine hoes recorded in the workshops could be considered as digging tools used to penetrate less compact soil and remove debris from shallow excavations to allow better access to flint. In the lack of contextual evidence other than from quarry sites this interpretation must be considered preliminary.

The specialized nature of the workshops, focused on the production of flint knives and a smaller number of cleavers, indicates an organized supply system rather than an incidental provision of stone tools by an impoverished social group (Graves-Brown, 2010:129). The similar opinion is implied by the title “Chert for the Masses ...” of the article by Klaunzer and his co-workers (Klaunzer *et al.*, 2017). We believe that the kind of tools and the manner of their provision, also suggest they were manufactured and distributed for general rather than specialized use. We imagine that for major construction projects, a supply of flint tools would be organized on a larger scale. It seems likely that the sizable mining shafts documented in the Wadi el-Sheikh complex could be associated with the large scale production and provision of tools for specific and highly organized work teams.



Figure 2. Preform of a cleaver, AM E9582, 20 cm long, 658 g. Scale 5 cm.

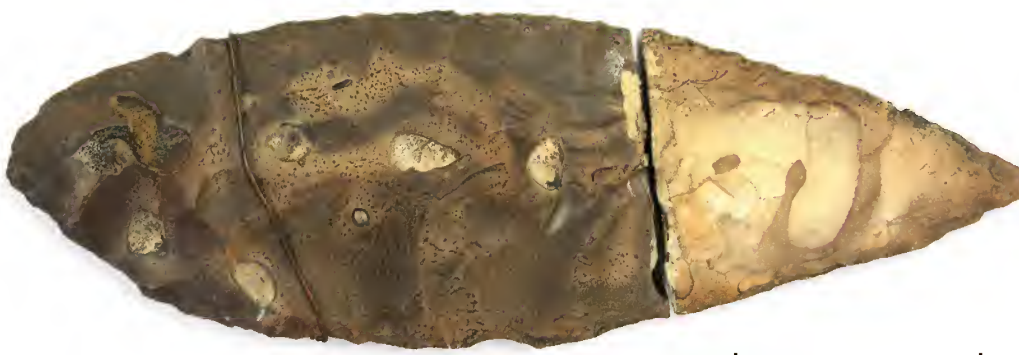


Figure 3. Knife, AM E9617, 19 cm long, 170 g. Scale 5 cm.



Figure 4. Preform of a knife, AM E9616, 21.5 cm long, 332 g. Scale 5 cm.



Figure 5. Knife, AM E9681, 23 cm long, 222 g. Scale 5 cm.



Figure 6. Preform of a knife, AM E9595, 24 cm long, 450 g. Scale 5 cm.



Figure 7. Knife-fragment, AM E9637, 8.5 cm long, 34 g. Scale 5 cm.



Figure 8. Knife-fragment, AM E9639, 9.5 cm long, 44 g. Scale 5 cm.



Figure 9. Preform of crescent knife, AM E9581, 17 cm long, 330 g. Scale 5 cm.

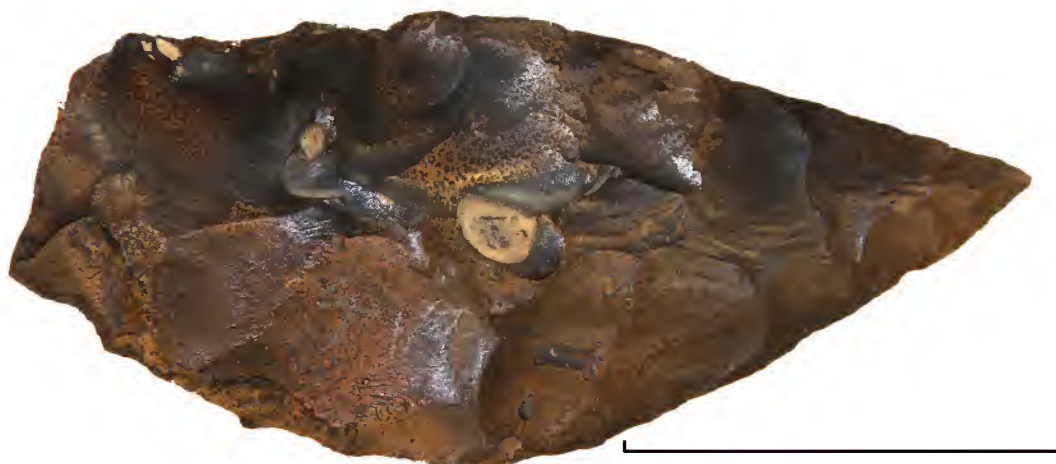


Figure 10. Fragment of a short knife, AM E9627, 12.5 cm long, 82 g. Scale 5 cm.



Figure 11. Fragment of crescent knife, AM E9666, 15.5 cm long, 190 g. Scale 5 cm.

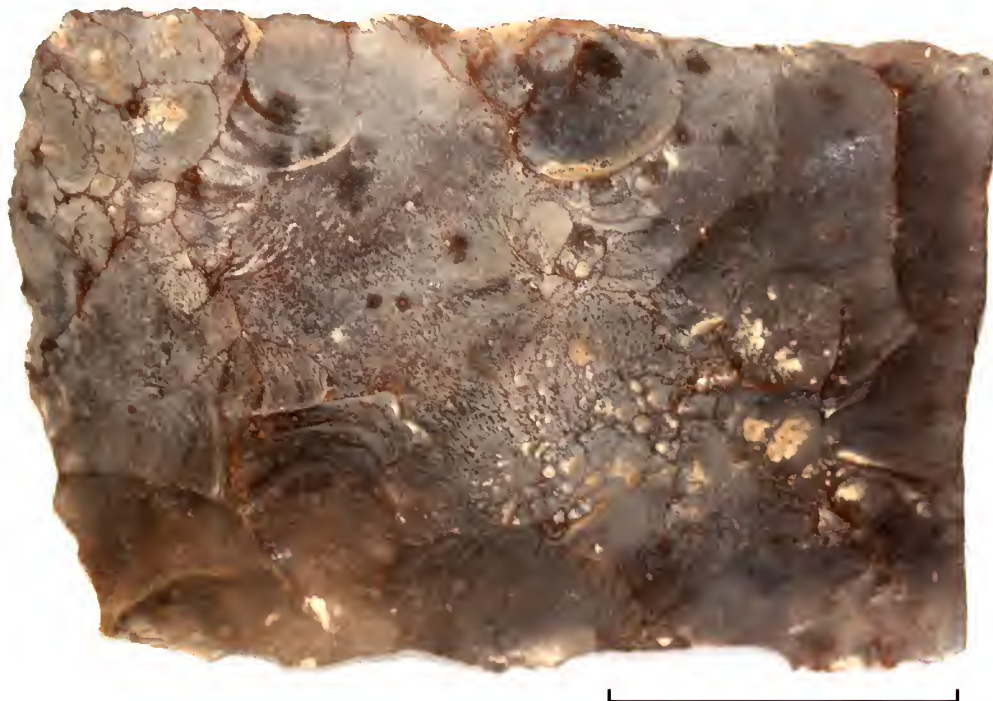


Figure 12. Fragment of a cleaver, AM E9692, 13 cm long, 344 g. Scale 5 cm.



Figure 13. Advanced preform of a cleaver, AM E9602, 23.5 cm long, 722 g. Scale 5 cm.



Figure 14. Preform of a pick with crest, AM E9661, 21 cm long, 848 g. Scale 5 cm.



Figure 15. Pick, AM E9653, 21 cm long, 482 g. Scale 5 cm.

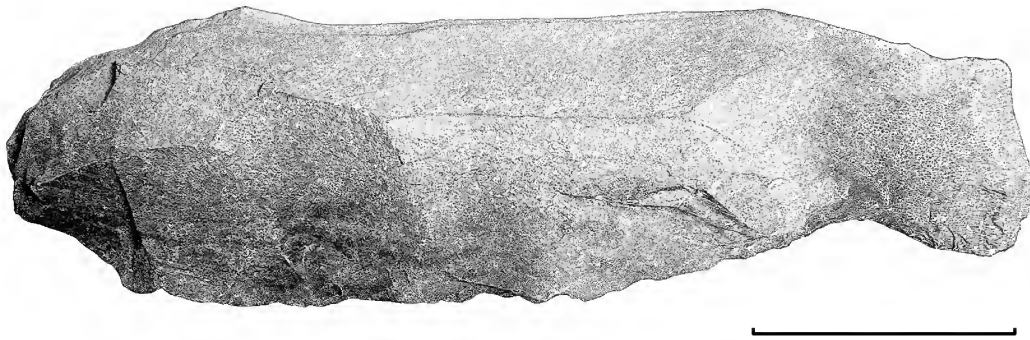


Figure 16. Pick, MV X6810, 19 cm long, 594 g. Scale 5 cm.



Figure 17. Hoe, AM E9660, 13 cm long, 250 g. Scale 5 cm.

ACKNOWLEDGMENTS. We wish to thank several people who made this study possible, including Dion Peita, Collection Coordinator at the Australian Museum for providing financial support and encouragement; Dr Elizabeth Bonshek, Senior Curator for Pacific Cultures, and Penelope Iking, Collection Manager for International Indigenous Collections at the Museum Victoria for access and assistance in studying material under their care; Dr Alfred Pawlik from the University of the Philippines Diliman for sharing with us his observations at Wadi el-Sheikh Quarry; Dr Val Attenbrow from the Australian Museum for insightful comments; two reviewers who helped to improve this paper; Allison Dejanovic for her support and lending us equipment, Charlotte Kowalski and Vickie Tran for their assistance in processing data and images; Jane Roy, Peter Dadswell and Penny Zylstra for generous help in editing. All photos and a digital drawing (Fig. 16) were produced by Stan Florek.

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Endnotes

- 1 A few Levallois cores are present in the MV collection—compare Kobusiewicz, 2006:458; Köhler *et al.*, 2017.
- 2 A few flakes are from “foreign” flint and/or clearly associated with Palaeolithic. One flake, resulting from reduction process is in the AM assemblage.
- 3 One pick in Graves-Brown (2010:565) is assigned to the New Kingdom after Seton-Karr (1905)—it is far larger than any in our assemblages in AM and MV but similar in morphology.
- 4 Excluding Neolithic and Palaeolithic use of the site.
- 5 Lack of terminological consistency makes this tool category less visible and not systematically described and classified, along with some other bifacial artefacts of the Neolithic and Bronze-age periods (Holmes, 1989:395).
- 6 Somewhat similar tools were associated with a gold mine at Bakari and described as the earliest type of mining tools (Rothenberg *et al.*, 1998:7, fig. 4), however the nature of the published evidence makes it difficult to compare them systematically with our picks.
- 7 As we do not have qualitative and quantitative data on other workshop-assemblages collected by Seton-Karr.
- 8 Unless they were discarded at the construction site where the excavation was performed (Seton-Karr, 1905).

Species of Heterolepismatinae (Zygentoma: Lepismatidae) Found on some Remote Eastern Australian Islands

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ABSTRACT. Lepismatid silverfish found on Norfolk Island, Lord Howe Island, Balls Pyramid and the Herald Cays are examined. Despite their isolated locations and small land area, these islands each support one or two species of the genus *Heterolepisma* Escherich. A phylogenetic analysis based on 23 morphological characters conducted using 14 adequately described Heterolepismatinae revealed deep rooted phylogenetic divergences and a new genus *Maritisma* is erected for *M. coralinium* sp. nov.; *Heterolepisma dispar* Uchida from Japan is transferred to the new genus. *Heterolepisma howense* Womersley is redescribed from the type material and additional specimens from Lord Howe Island; it is also the only species of *Heterolepisma* so far found on Norfolk Island. *Heterolepisma milledgei* sp. nov. is described from both Lord Howe Island (including Blackburn Island in its lagoon) and Balls Pyramid. *Heterolepisma pyramidum* sp. nov. is described from Balls Pyramid. *Maritisma coralinium* gen. nov., sp. nov. and *H. heraldense* sp. nov. are described from the Herald Cays; both are considered as endangered by rising sea level however *H. heraldense* sp. nov. may be conspecific with the inadequately described *H. rouxi* Silvestri from New Caledonia. Limited molecular data (COI and 28S) were obtained for two of the Lord Howe Island/Balls Pyramid species.

Introduction

Silverfish are primitively wingless and generally found in drier or subterranean habitat, and so would seem to be unlikely seafarers but their occurrence on numerous isolated islands suggests otherwise. Silverfish have been collected on many Atlantic islands such as the Canary Islands (e.g., Mendes *et al.*, 1993, Molero-Baltanás *et al.*, 2014), throughout the Caribbean island chain (e.g., Wygodzinsky, 1972, Espinasa *et al.*, 2011), on islands of the Indian Ocean e.g., the Seychelles (Carpenter, 1916) and throughout the Pacific including Hawaii (e.g., Zimmerman, 1948) and Japan (e.g., Uchida, 1944). Silverfish of the genus *Heterolepisma* Escherich, 1905, in particular, seem to be particularly widely distributed on islands throughout the Pacific with *H. annectens* described from the Juan Fernandez Islands (Silvestri, 1924), *H. howense* from

Lord Howe Island (Womersley, 1942), *H. insulare* from the Galapagos (Banks, 1901), *H. japonicum* from Ishigaki Island in the Okinawa group (Uchida, 1968), *H. mumfordi* from the Marquesas (Silvestri, 1935), *H. rouxi* from New Caledonia (Silvestri, 1915), *H. tonga* from Tonga (Mendes, 2012) and *H. zelandicum* from New Zealand (Tillyard, 1924). This paper describes a surprisingly rich and diverse fauna from several islands, all several hundred kilometres off the east coast of Australia (Fig. 1). These include Lord Howe Island (600 km from the Australian mainland, 14.5 km² land area), Norfolk Island (land area 35 km², 1400 km from the Australian mainland and 900 km from Lord Howe Island), Balls Pyramid, a volcanic stack (land area ca 0.3 km²) rising 562 m above the ocean some 20 km to the south of Lord Howe Island and the Herald Cays, two low-lying coral atolls (combined land area 0.34 km², some 300 km east of Cairns and 1,700 km northwest of New Caledonia).

Keywords: Thysanura; taxonomy; zoogeography; new genus; new species; DNA barcodes; 28S rDNA; threatened species

Taxonomic registration: (LSID publication) <http://zoobank.org/CB380F40-F8D8-471B-86B5-E567C8B8EEC9>

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Received: 9 April 2019 **Accepted:** 2 July 2019 **Published:** 24 July 2019 (in print and online simultaneously)

Publisher: The Australian Museum, Sydney, Australia (a statutory authority of, and principally funded by, the NSW State Government)

Citation: Smith, Graeme B., and Andrew Mitchell. 2019. Species of Heterolepismatinae (Zygentoma: Lepismatidae) found on some remote eastern Australian Islands. *Records of the Australian Museum* 71(4): 139–181. <https://doi.org/10.3853/j.2201-4349.71.2019.1719>

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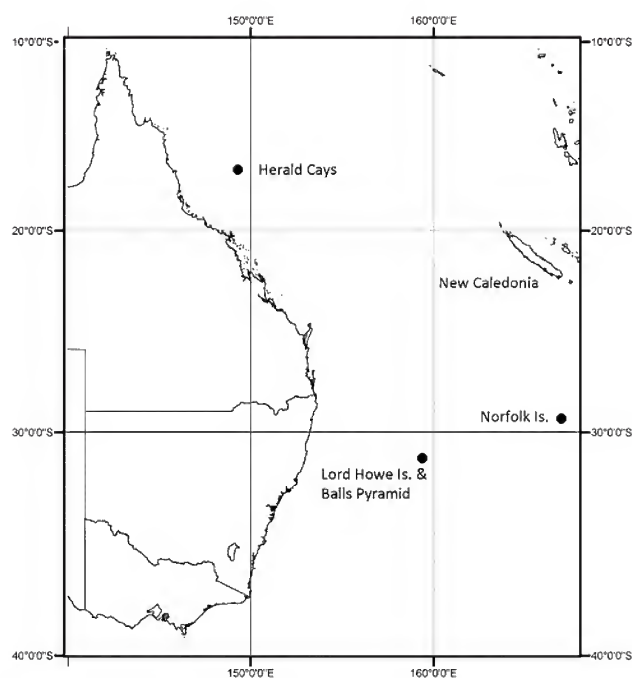


Figure 1. Collection localities.

There has been confusion over the gender of the name *Lepisma* and more particularly over genus names derived from *Lepisma* (Molero-Baltanás *et al.*, 2015). The International Commission of Zoological Nomenclature has recently ruled that *Lepisma* and all genus names derived from *Lepisma* should be treated as of neuter gender (ICZN, 2018). Names affected by this decision included in this work have been corrected.

Materials and methods

Most specimens are deposited in the entomological collection of the Australian Museum in Sydney (AMS) and have been allocated museum data base numbers prefixed “K.” in the lists of material examined. The specimen of *Qantelsella louisae* Smith is deposited in the Queensland Museum and has a specimen number T228755. The specimen of *Acrotelsella erniei* Smith is deposited in the Northern Territory Museum and Art Gallery has a specimen number of NT33287. Specimen numbers prefixed “gbs” are privately databased (GBS).

Locality co-ordinates are mostly taken from Google Earth although co-ordinates of recently collected material were measured with a hand-held GPS unit. Some recent specimens were collected in 100% ethanol so that DNA could be extracted, but the remaining specimens, held in 80% ethanol were considered too old to yield useful DNA sequences using currently available techniques. Either a leg was removed for DNA extraction or the whole specimen was soaked in DNA extraction buffer containing proteinase-K prior to dissection and slide mounting using the methodology outlined in Smith *et al.*, 2019.

Roman numerals are used to indicate abdominal segment number. In addition, the following abbreviations are used: AM: Australian Museum, 1 William St, Sydney 2010 Australia; asl: above sea level (m); HW: head width (mm); H+B: head and body length (mm); K2P: Kimura 2-parameter; L/W: length to width (ratio); NSW: New South Wales; PI, PII, PIII: legs of prothorax, mesothorax and metathorax

respectively; penult: penultimate, referring to second last article of maxillary palp; ult: ultimate (referring to last article of the palps). The prefixes pro, meso and meta are affixed to thoracic characters such as sterna, tibia and tarsus.

Specimens are currently stored in 80% ethanol/water unless specifically mentioned as being in 100% ethanol or else mounted on slides. Dissected specimens were each mounted on one or two slides using Tendeiro medium, with the head and thorax mounted on one slide and the abdomen on a second slide or the whole specimen on a single slide if small. Each slide of material stored in the Australian Museum has its own unique specimen number.

The term *macrochaetae* refers to the larger stronger bristles, *setae* refers to smaller thinner bristles (usually simple), *setulae* to the very small, usually straight, setae and *cilia* to the curly thin hairs, often associated with the combs, setal collar or notal margins. Left and right refer to the animal when the dorsal surface is observed with the head forward. Basiconic sensilla on the antennae and palps are described using the terminology of Adel (1984). Terminology for the “segments” of the antennae, terminal filaments and ovipositor follows that explained in Smith (2015) where the term *annulus* will be used for each single unit of the flagellum (excluding pedicel and scape), usually a widened region carrying a single rosette of setae (but occasionally with a smaller secondary rosette), *T-annulus* for each annulus bearing a trichobothrium, *interval* for the group of annuli between T-annuli with the T-annulus being the most distal annulus of the interval. For the terminal filaments and ovipositor, the term *division* will be used for each “segment” defined by a visible suture, albeit often faint.

Character analysis

It was not possible to include *H. andinum* Silvestri, *H. annectens* Silvestri, *H. bisetosum* (Carpenter), *H. dispar* Uchida, *H. exactum* Silvestri, *H. horni* Stach, *H. insulare* Banks, *H. japonicum* Uchida, *H. kraepelini* Silvestri, *H. michaelsoni* Silvestri, *H. mossambicense* Mendes, *H. mumfordi* Silvestri, *H. pampeanum* Silvestri, *H. primafrum*, *H. rouxi* Silvestri, *H. stilivarians* Silvestri, *H. tonga* Mendes, *H. trisetosum* (Escherich) and *H. zelandicum* Tillyard in the character analysis due to the lack of information on at least one character (usually the chaetotaxy of the anterior margin of the frons and labrum and the presence of lanceolate and/or triangular scales). Mendes (pers. comm. 2018) has, however, confirmed that *H. tonga* and *H. mossambicense* have lanceolate scales on the femora and lack macrochaetae along the anterior margin of the frons. *Anisolepisma aquilonaridum* Smith is included as the outgroup in this analysis.

The character matrix in Table 1 was analysed in PAUP*4.0 (Swofford, 2002) using a branch-and-bound search.

Sampling, DNA extraction, PCR and DNA sequencing

Table 2 lists the nine DNA voucher specimens new to this study, and their associated BOLD and GenBank accession numbers. The remaining DNA sequences were already reported in Smith *et al.*, 2019.

DNA extractions used the Bioline Isolate II Genomic DNA Kit (Bioline, Eveleigh, NSW) following the manufacturers’ protocols, with exceptions noted below.

Table 1. Character states of *Anisolepisma* and some Heterolepismatinae (*Maritissima* gen. nov. and *Heterolepisma*).

character	<i>A. aquilonaridum</i>	<i>M. cordalinum</i> sp. nov.	<i>H. heraldense</i> sp. nov.	<i>H. parvum</i>	<i>H. pyramidum</i> sp. nov.	<i>H. serranoi</i>	<i>H. buntonorum</i>	<i>H. cooloola</i>	<i>H. howense</i>	<i>H. highlandi</i>	<i>H. sclerophyllum</i>	<i>H. coorongoooba</i>	<i>H. milledgei</i> sp. nov.	<i>stilvians</i> group sp. 1	<i>stilvians</i> group sp. 2
A	2	1	0	0	0	0	1	0	0	1	1	1	1	0	0
B	1	2	1	1	1	1	1	1	1	1	1	1	1	2	2
C	0	0	1	1	1	1	0	1	1	1	0	0	0	[0,1]	[0,1]
D	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
E	0	0	[1,2]	[1,2]	[1,2]	2	2	2	2	2	2	2	2	1	1
F	4	2	0	0	0	0	0	0	[0,1]	0	0	0	0	3	2
G	0	2	1	1	1	1	1	1	1	1	1	1	1	1	1
H	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
I	1	1	2	2	1	2	1	2	1	1	2	2	2	2	1
J	0	0	0	2	0	1	2	2	0	0	0	0	0	0	0
K	0	1	1	1	1	1	0	1	0	0	1	1	1	2	1
L	0	1	1	1	1	1	1	1	0	0	1	1	1	3	1
M	0	1	1	1	1	1	2	1	1	1	1	1	1	3	3
N	4	3	3	2	2	3	3	2	2	2	2	2	2	2	2
O	2	1	1	1	1	2	1	1	1	1	2	2	2	1	1
P	0	2	1	0	1	1	0	0	1	0	0	0	1	0	0
Q	2	3	2	2	2	2	0	0	0	0	0	0	0	0	0
R	4	3	2	2	2	1	1	1	1	1	1	1	1	1	1
S	4	2	2	2	2	1	1	1	1	1	1	1	1	1	1
T	0	0	2	1	2	2	1	2	2	0	2	1	2	7	5
U	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0

Key to character states: **A**, chaetotaxy of anterior margin of frons (glabrous=0, full row=1, large bushes=2); **B**, labrum (setae only = 1, many short macrochaetae=2); **C**, lanceolate scales (absent=0, present=1); **D**, triangular scales (absent=0, present=1); **E**, type of flower-like sensilla on ultimate article of maxillary palp of male (absent=0, slender=1, wide=2); **F**, arrangement of labial palp papillae (3+2 in curved cluster=0, 3+2 in two straight lines=1, 3+2 alternated in almost straight line=2, all five papillae in single straight line=3, four papillae in diamond arrangement=4); **G**, pronotal collar (absent=0, complete=1, medially interrupted=2); **H**, prothorax with 1+1 isolated anterior tufts of macrochaetae (absent=0, present=1); **I**, number of macrochaetae in posterior combs of nota (absent=0, one=1, two macrochaetae=2); **J**, location of macrochaeta of the anterior trichobothrial area of pronotum (absent=0, laterad of trichobothrium=1, mediad of trichobothrium=2); **K**, number of combs on mesonotum with two or more macrochaetae (none=0, one to three=1, four to five=2, greater than five=3); **L**, number of combs on metanotum with two or more macrochaetae (none=0, one to three=1, four to five=2, greater than five=3); **M**, shape of prothoracic sternum (not free=0, triangular or cordiform=1, parabolic=2, trapezoidal=3); **N**, chaetotaxy of urotergite I (1+1 combs=1, 2+2 combs (lacking submedial)=2, 3+3 combs=3, 2+2 combs (lacking sublateral)=4); **O**, number of macrochaetae in submedial combs of urotergites (one or usually one=1, always two=2); **P**, shape of urotergite X in male (long, parabolic=0, trapezoidal=1, very short, round=2); **Q**, chaetotaxy of urostermite I (glabrous=0, medial comb of 2-5 macrochaetae=2, medial comb of >6 macrochaetae=3); **R**, chaetotaxy of urostermite II (glabrous=0, 1+1 single macrochaetae=1, 1+1 combs of 2-5 macrochaetae=2, 1+1 combs of >6 macrochaetae=3, 1+1+1 combs=4); **S**, urostermite II-VII (1+1 single macrochaetae=1, 1+1 combs each of more than one macrochaetae=2, 1+1+1 combs present on some urostermites=3, 2+1+2 combs present on some urostermites=4); **T**, urostyli (IX only in both sexes = 0, VIII+IX in ♀ and IX only in ♂ = 1, VII-IX in ♀ and VIII-IX in ♂ = 2, VIII-IX in both sexes=3, VII-IX in both sexes = 4, VI-IX in both sexes = 5, V-IX in both sexes = 6, IV-IX in both sexes = 7); **U**, macrochaetae of urosternal combs packed close together=0, macrochaetae spaced apart=1. Two values in square brackets indicate uncertainty exists between the two states indicated.

In general, whole specimens collected directly into 100% ethanol, were soaked in 180 µL of DNA extraction buffer and 20 µL of proteinase-K at room temperature for 1–3 hours. The remaining cuticle was returned to 100% ethanol and later dissected in 80% ethanol and mounted on to two slides using Tendeiro medium (head and thorax on one slide, abdomen on the other). Polymerase Chain Reaction (PCR) amplification of the DNA barcode region of the mitochondrial COI gene used the primers and followed the method of Mitchell (2015). For the 28S rDNA D9–D10 region, we used one forward (28S_8fm) and two reverse PCR primers (28S_10rm and 28S_11rm), which were simply 5'–M13-tailed versions of

Machida and Knowlton's (2012) primers [28S] #8, [28S] #10_RC and [28S] #11_RC, respectively. PCR conditions for both genes followed those reported in Mitchell (2015) for COI. PCR products were purified using ExoSAP and sequenced in both directions using ABI Big Dye Terminator v.3.1 chemistry by Macrogen Inc. (Seoul, South Korea).

DNA sequence assembly and phylogenetic analysis

Forward and reverse direction sequence trace files were assembled using Geneious v. 9.1.8 (Kearse et al., 2012) and

Table 2. DNA sequences derived in this study and their voucher specimens.

museum ID	sample ID	BOLD process ID	species	locality	GenBank accession (COI)	GenBank accession (28S)
K.261293	gbs004182	ZYII076-18	<i>Heterolepisma howense</i>	Norfolk Island	MN133046	MN150477
K.261254	gbs005494	ZYIII002-19	<i>H. pyramidum</i> sp. nov.	Balls Pyramid	MN133049	MN150480
K.261256	gbs005492	ZYIII001-19	<i>H. milledgei</i> sp. nov.	Blackburn Island	MN133048	MN150479
K.261349	gbs005497	ZYII196-18	<i>H. milledgei</i> sp. nov.	Balls Pyramid	MN133047	n/a
K.261258	gbs005499	ZYIII004-19	<i>H. milledgei</i> sp. nov.	Balls Pyramid	MN133051	MN150482
K.377827	gbs005496	ZYIII003-19	<i>H. milledgei</i> sp. nov.	Balls Pyramid	MN133050	MN150481
K.377884	gbs002975	ZYII053-18	<i>H. parvum</i>	Barrow Island	n/a	MN150476
K.377883	gbs002980	ZYIII005-19	<i>H. parvum</i>	Barrow Island	n/a	MN150483
K.377882	gbs002982	ZYIII006-19	<i>H. parvum</i>	Barrow Island	n/a	MN150484

consensus sequences were aligned using Muscle (Edgar, 2004) and adjusted by eye. DNA sequences, sequence trace files, and specimen collection data were uploaded to BOLD (Ratnasingham and Hebert, 2007) and can be downloaded from public project ZYIII (Zygentoma of Australia III). New sequences were submitted to GenBank (Table 2).

Three data sets were constructed: one for each of the two genes alone, and a concatenated alignment of samples which had data for both genes. Both COI and 28S alignments had sequence trimmed from the 3'-ends to minimize missing data before phylogenetic analysis; 21 bp and 211 bp were trimmed, respectively.

FABOX v. 1.4.2 (Villesen, 2007) was used to edit sequence names. MEGA v. X (Kumar et al., 2018) was used to calculate genetic distances. The remaining phylogenetic analyses were performed on the CIPRES v.3.3, online analytical platform (Miller et al., 2010). Partitionfinder v.2 (Lanfear et al., 2016) was used to select partitioning schemes and the most appropriate models of sequence evolution. Bayesian Inference (BI) was performed using MrBayes 3.2.6 (Ronquist et al., 2012) and maximum likelihood analyses using RAxML v8.2.10 (Stamatakis, 2014).

The MrBayes analysis was set to run for 30 million generations, with a sample frequency of 1,000, using two runs, setting the number of chains to four. The stopping rule was used to cease the analysis when the average standard deviation of split frequencies dropped below 0.01, indicating convergence of the chains. The burnin fraction was set to 0.25. RAxML analysis used the hill climbing algorithm with 1,000 rapid bootstrap replicates. *Ctenolepisma longicaudatum* Escherich was used as the outgroup.

Morphometric data

Measurement data of whole specimens in alcohol and dissection used the methods described in Smith (2013). Measurements of L/W of the processes of coxites IX, urotergite X and the thoracic sternites as well as the size of the gap relative to the average length of the combs on the metasternite were made from *camera lucida* drawings of slide mounted material. Morphometric data for *H. howense* and *H. milledgei* sp. nov. were compared with the data presented in Smith et al., 2019 (p. 10, table 2) for the *H. sclerophyllum* species complex and *H. cooloola*.

The numerous types available for the redescription of *H. howense* were all very pale after so many years in alcohol. Four specimens were dissected and mounted on slides but had lost most setae and almost all scales, characters were faded

and were very difficult to illustrate. For its redescription, most illustrations are of a more recently collected Lord Howe Island specimen (K.541011, K.541012). As each illustration was completed it was compared in detail with all slide mounted material (including types, non-type material from Lord Howe Island and also material from Norfolk Island) to confirm no significant differences exist.

Results

Character analysis

The character analysis (Fig. 2) gives moderate support for the creation of a new genus for one of the Herald Cay species, which is described below as *Maritisma coralinium* gen. nov., sp. nov.

Analysis of the morphology matrix yielded six most parsimonious trees with a length of 61 steps, each with a consistency index of 0.66 and retention index of 0.61. The strict consensus tree, shown in Fig. 2, recovered three species groups: the *H. sclerophyllum* species group (*H. sclerophyllum*, *H. coorongooba* and *H. milledgei* sp. nov.), the *H. pyramidum* group (*H. pyramidum* sp. nov., *H. serranoi*, *H. parvum* and *H. heraldense* sp. nov.) and the *H. stilivarians* group. Analysis also placed *Maritisma coralinium* sp. nov. as a sister group to the *H. stilivarians* group. The relationship between the latter species is the result of them sharing character state C, where the labrum bears many short apically bifurcate macrochaetae rather than simple setae. *Maritisma coralinium* sp. nov. is however strikingly different to the *H. stilivarians* species group in many other characters and it is difficult to envisage a close relationship. Molecular data could eventually clarify this situation but it will be necessary to obtain fresh material.

Molecular data

Table 2 lists the BOLD and GenBank accession numbers of the new sequences reported here, i.e. six COI sequences and eight 28S sequences. The remaining sequences in the data sets comprise the entire DNA data sets from Smith et al. (2019), thus the combined COI and 28S (concatenated) data set comprises 35 taxa, while the COI only and 28S only data sets each comprise 50 taxa.

The MrBayes analysis ran for 22.245 million generations, until the run was stopped when the convergence statistic (average standard deviation of the splits frequencies) dropped below 0.01. Figure 3 shows the Bayesian tree obtained for the concatenated data set. The Bayesian trees

resulting from analysis of COI only and 28S (Figs 209, 210, at end of this work: pp. 178–179).

Figure 3 shows that, *H. pyramidum* sp. nov. is placed close to the *H. cooloola* group. Both species lack macrochaetae along the anterior margin of the frons and have lanceolate scales on the femora, tibia, clypeus and terminal filaments. The clade containing *H. highlandi* also appear to have lanceolate scales at least on the terminal filaments but has macrochaetae along the anterior margin of the frons. All other *Heterolepisma* clades shown have macrochaetae along the anterior margin of the frons but lack lanceolate scales.

The *H. howense* 28S sequence (Fig. 210) is strongly divergent from the other *Heterolepisma*, with many point mutations rather than insertions/deletions. The divergence is less marked in COI and the concatenated data set.

For *H. parvum*, only 28S data was obtained. The species is placed well within *Heterolepisma* but is not strongly associated with any other species, and the three 28S sequences are identical.

Heterolepisma milledgei sp. nov. is placed within the *H. sclerophyllum* clade in agreement with its similar morphology. *Heterolepisma milledgei* sp. nov. is strongly divergent from other members of the *H. sclerophyllum* group in the COI data set (Fig. 209), forming a basal cluster within the group and with a minimum K2P distance of 14.2% to the closest member of another species. There is a K2P distance of 6.9–8.1% between the three specimens collected on Balls Pyramid and one collected on Blackburn Island (within the Lord Howe Island lagoon) however 28S sequences for all three specimens (two from Balls Pyramid and one from Blackburn Island) were identical.

Systematics

Family Lepismatidae Latreille, 1802

Subfamily Heterolepismatinae Mendes, 1991

Heterolepisma Escherich, 1905

Heterolepisma Escherich, 1905: 63.

Isolepisma Escherich, 1905: 61.

Notolepisma Tillyard, 1924: 242.

Type species: *Lepisma pampeana* Silvestri, 1902 by subsequent designation, see Paclt, 1967: 25.

Heterolepisma howense Womersley

Heterolepisma howensis Womersley, 1942:116.

Figs 4–41

Holotype. ♂ (HW 1.28) (K.263961 in alcohol) LORD HOWE ISLAND: Rocky Run, 31.55°S 159.09°E, iv.1942, Max Nicholls. **Paratypes.** 5♂♂ 8♀♀ 12 partial specimens and some fragments including allotype ♀ (HW 1.38) (K.263962 in alcohol) same data as holotype; 1♀ (HW 1.25) (K.541009 K.541010 on two slides) same data as holotype; 1♀ (HW ?) (K.261040 K.261041 on two slides) same data as holotype; 1♀ (HW 1.23) (K.261311 on slide) same data as holotype; 1♂ (HW ??) (K.261038, K.261039 on two slides) same data as holotype; 1 partial specimen (HW

1.30) (K.263963 in alcohol), same data as holotype (head, thorax and abdomen I–IV only); 1♀ (HW 1.21) (K.377841 in alcohol) same data as holotype; 1 partial specimen (HW 1.23) (K.377842 in alcohol) same data as holotype (head, thorax and abdominal segments I–III only); 1♂ (HW 1.10) (K.377843 in alcohol) same data as holotype; 1♀ (HW 1.25) (K.377844 in alcohol) same data as holotype; 1 partial specimen (HW 1.23) (K.377845 in alcohol) same data as holotype (head, thorax and abdominal segments I–IV only); 1♂ (HW 0.90) (K.377846 in alcohol) same data as holotype; 1♀ (HW 1.08) (K.377847 in alcohol) same data as holotype; 1♂ (HW 1.00) (K.377848 in alcohol) same data as holotype; 1 partial specimen (HW 1.00) (K.377849 in alcohol) same data as holotype (head, thorax and abdominal segments I–III only); 1♀ (HW 1.13) (K.377850 in alcohol) same data as holotype; 1 partial specimen (HW 1.18) (K.377851 in alcohol) same data as holotype (head, thorax and abdominal segments I–III only); 1 partial specimen (HW 1.08) (K.377852 in alcohol) same data as holotype (head, thorax and abdominal segments I–V only); 1 partial specimen (HW 1.15) (K.377853 in alcohol) same data as holotype (head, thorax and abdominal segments I–IV only); 1♂ (HW 1.18) (K.377854 in alcohol) same data as holotype; 1 partial specimen (HW ?) (K.377855 in alcohol) same data as holotype (thorax and abdominal segments I–VI only); 1 partial specimen (HW 1.00) (K.377856 in alcohol) same data as holotype (head, thorax and abdominal segments I–III only); 1 partial specimen (HW 1.04) (K.377857 in alcohol) same data as holotype (head, thorax and abdominal segments I–III only); 1 partial specimen (HW 1.03) (K.377858 in alcohol) same data as holotype (head, thorax and abdominal segments I–IV only); 1 juvenile ♀ (HW 0.83) (K.377859 in alcohol) same data as holotype; 1 partial specimen (HW 0.93) (K.377860 in alcohol) same data as holotype (head, thorax and abdominal segments I–III only); fragments (K.377861 in alcohol) same data as holotype.

Additional Lord Howe Island material examined. 1♂ (HW 1.20) (K.541011 K.541012 on two slides) LORD HOWE ISLAND: Goat House walking track, 350m from start, Intermediate Hill 31.554°S 159.080°E, 8.xii.2000, G. Cassis, LHI/GC/L 12d; 1♂ (HW 0.95) (K.377862 in alcohol) same data as previous (in two pieces); 1 juvenile (HW 0.68) (K.377865 in alcohol) LORD HOWE ISLAND: Point where walking trail first enters Erskine Valley from coast 31.574°S 159.072°E, 28.xi.2000, LHIS043/04B.

Non Lord Howe Island material examined. 1♂ (HW 1.11) (K.261293 K.261294 on two slides) NORFOLK ISLAND: Birdrock track, National Park, 29.01°S 167.94°E, 26.x.2013, A. Wells, L. Mound LAM5845; 1 juvenile (HW 0.59) (K.377824 in alcohol) same data as previous; 1♀ (HW 1.13) (K.377825 in alcohol) NORFOLK ISLAND (not further specified), 22–29.x.1967, C. N. Smithers; 1♂ (HW 0.95) (K.261290 K.261291 on two slides) same data as previous; 1♂ (HW 0.93) (K.377826 in alcohol) same data as previous; 1 damaged ♀ (most of head and pronotum broken off) (K.261292 on one slide) same data as previous.

Diagnosis. This species can easily be distinguished from other described species of *Heterolepisma* with a glabrous anterior margin on the frons, a glabrous urosternite I, 1+1 single macrochaetae on urosternites II–VII, three pairs of styli in the female and two in the male (i.e. *H. cooloola* Smith *et al.*, 2019, and also possibly the inadequately described

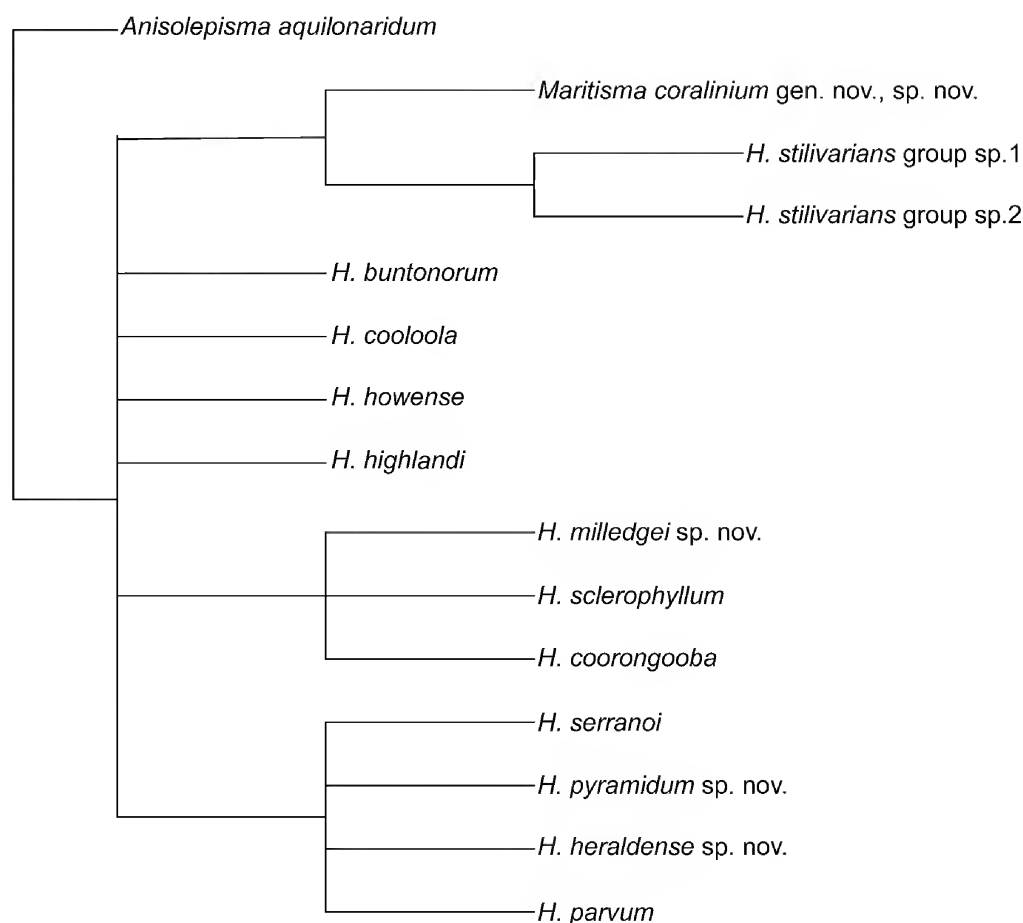


Figure 2. Morphology-based parsimony tree.

H. kraepelini Silvestri, 1908) by its trapezoidal urotergite X, by the absence of a macrochaeta mediad of the anterior trichobothrium of the pronotum, by the absence of combs of two macrochaetae on the meso- and metanota, by the absence of a smaller secondary macrochaeta in the posterior combs of the nota and urotergites.

Redescription

Appearance: Medium sized silverfish, thorax about 15% wider than abdomen which only tapers slightly posteriorly from about the fifth abdominal segment; appearance when live unknown.

Body length: Maximum H+B 8.4 mm; HW 1.38 mm; thorax: length 2.7 mm or 0.33 H+B (range 0.30–0.39); width up to 2.1 mm with no great difference in length or width between the pro, meso- and metanota although the pronotum is the narrowest; most antennae lost, maximum preserved 0.7 H+B (about 0.5 H+B in the original description); terminal filaments also mostly lost (0.8 H+B in original description).

Pigmentation: Pigment completely faded in all type material; the following description of pigmentation was made using specimen K.541011 before it was dissected. Pigment pinkish/brown but can vary considerably between specimens. Flagellum of antennae evenly pale becoming slightly darker distally; pedicel and scape without pigment. Scape with pinkish pigment on external face. Terminal filaments annulated darker brown with the most distal annulus of

each major division completely lacking pigment. Head with pigment around eyes and along sides of head to the antennae and among the peri-antennal macrochaetae. Clypeus, labrum and mandibles without pigment. Maxillary palp with light pink pigment along sides of ultimate article and similar but darker pigment on the penultimate article, less on the third article and very little on the first two articles. Labial palp largely without pigment. Legs with slight pigment on anterior “shoulder” of coxae, absent from trochanter, slight pigment on the posterior bulge and distal dorsal apex of femur, tibia with light pigment which is slightly stronger proximally and somewhat stronger again distally near dorsal margin, darkish pigment on first tarsal article only. Urotergite X with pigment in basal lateral region.

Macrochaetae: Smooth, hyaline or slightly straw coloured, apically bifurcate with truncated tips to each bifurcation. Some macrochaetae on tibia, stout carrot-shaped.

Scales: Quite broad, hyaline or with brown ribs, with numerous subparallel ribs that do not surpass the margin of the scale (Fig. 4). Scales found on top of head, protruding well forward over the margin in the medial region; round scales absent from clypeus and labrum as well as from all cephalic appendages and styli; present on all nota, all thoracic sterna, and coxae of legs but absent from remaining leg articles, present on all urotergites and urosternites. Lanceolate scales (Fig. 5) present on clypeus, femora, tibia, basal divisions of cerci and probably also on scape.

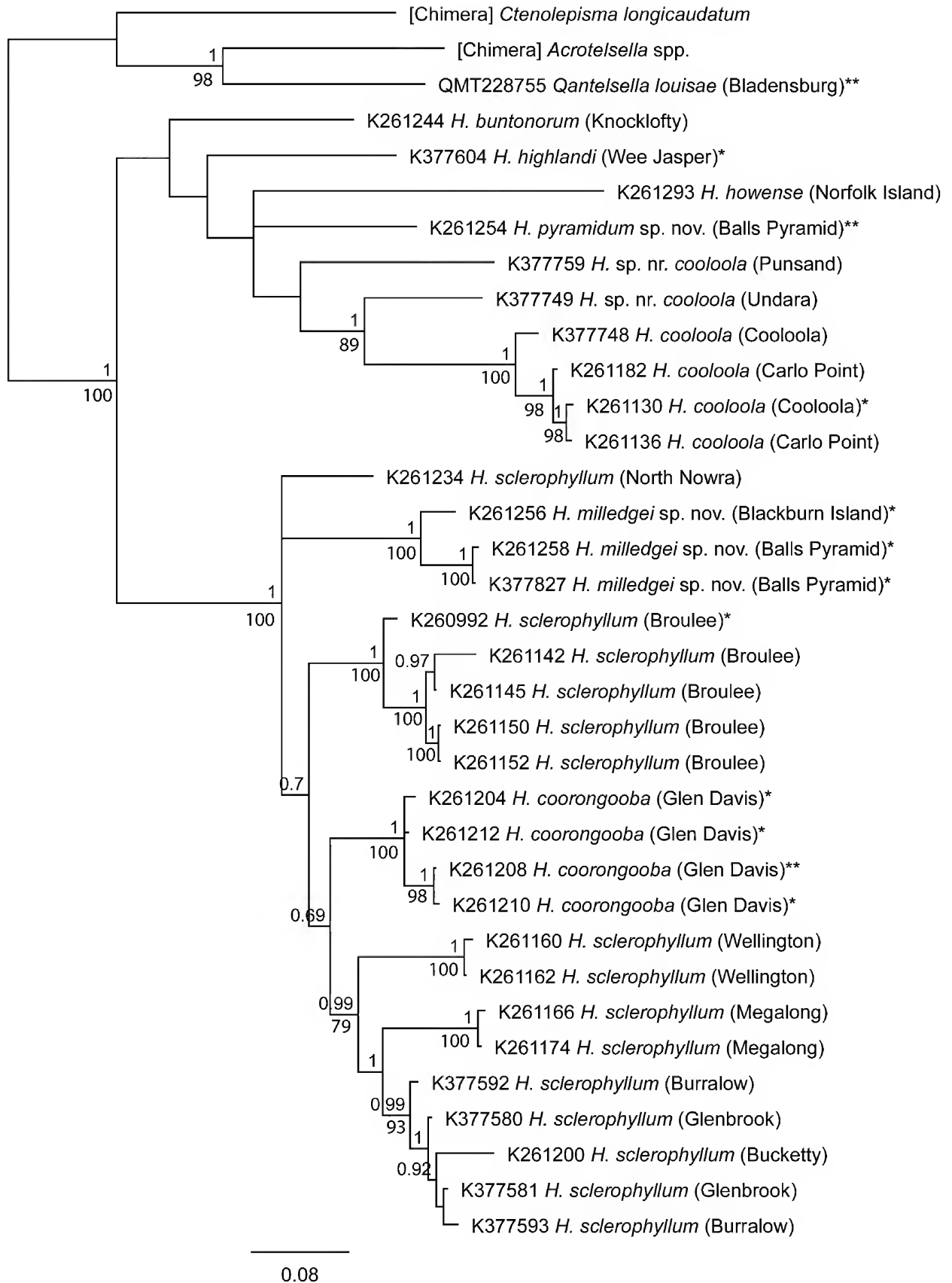
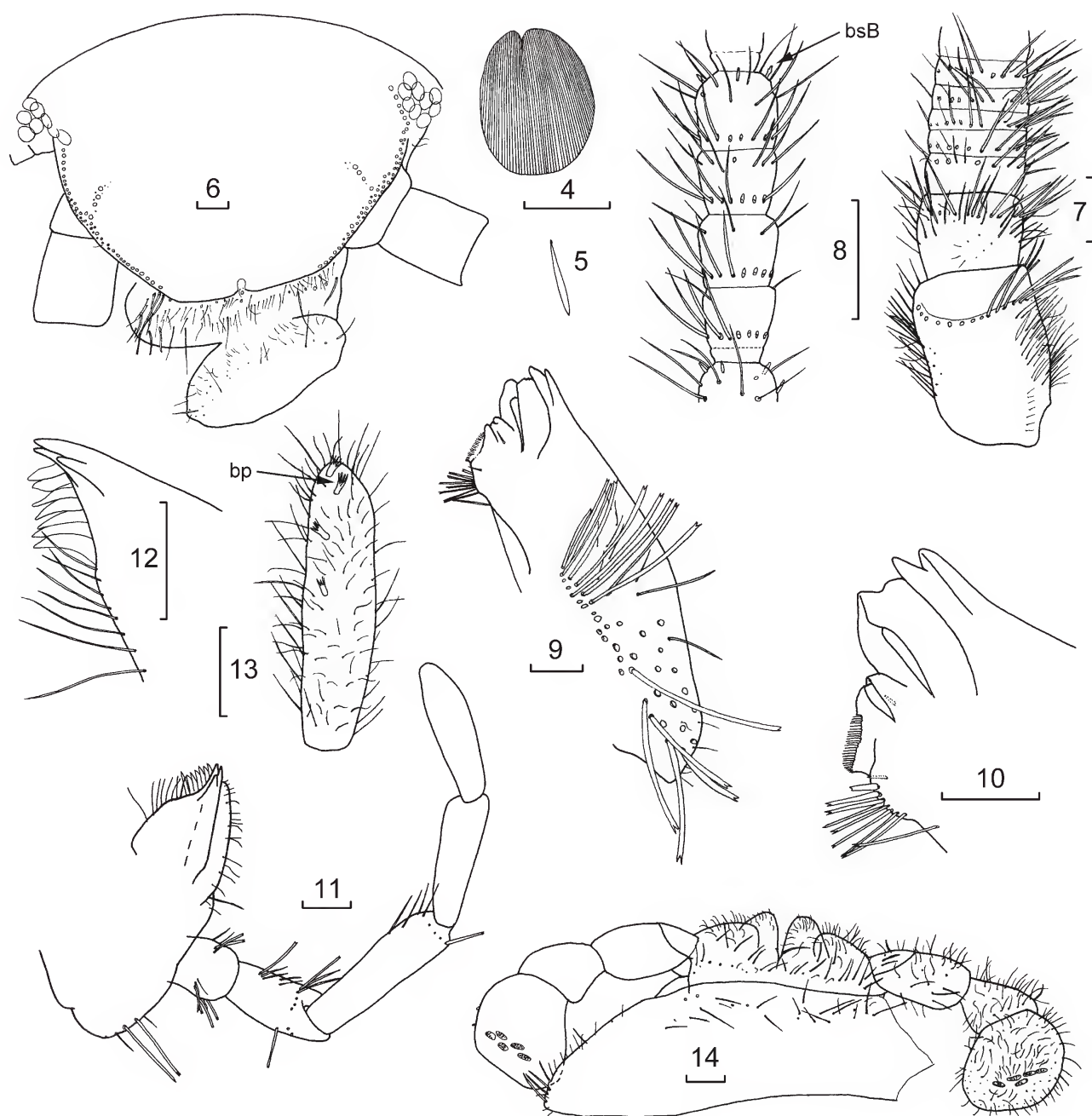


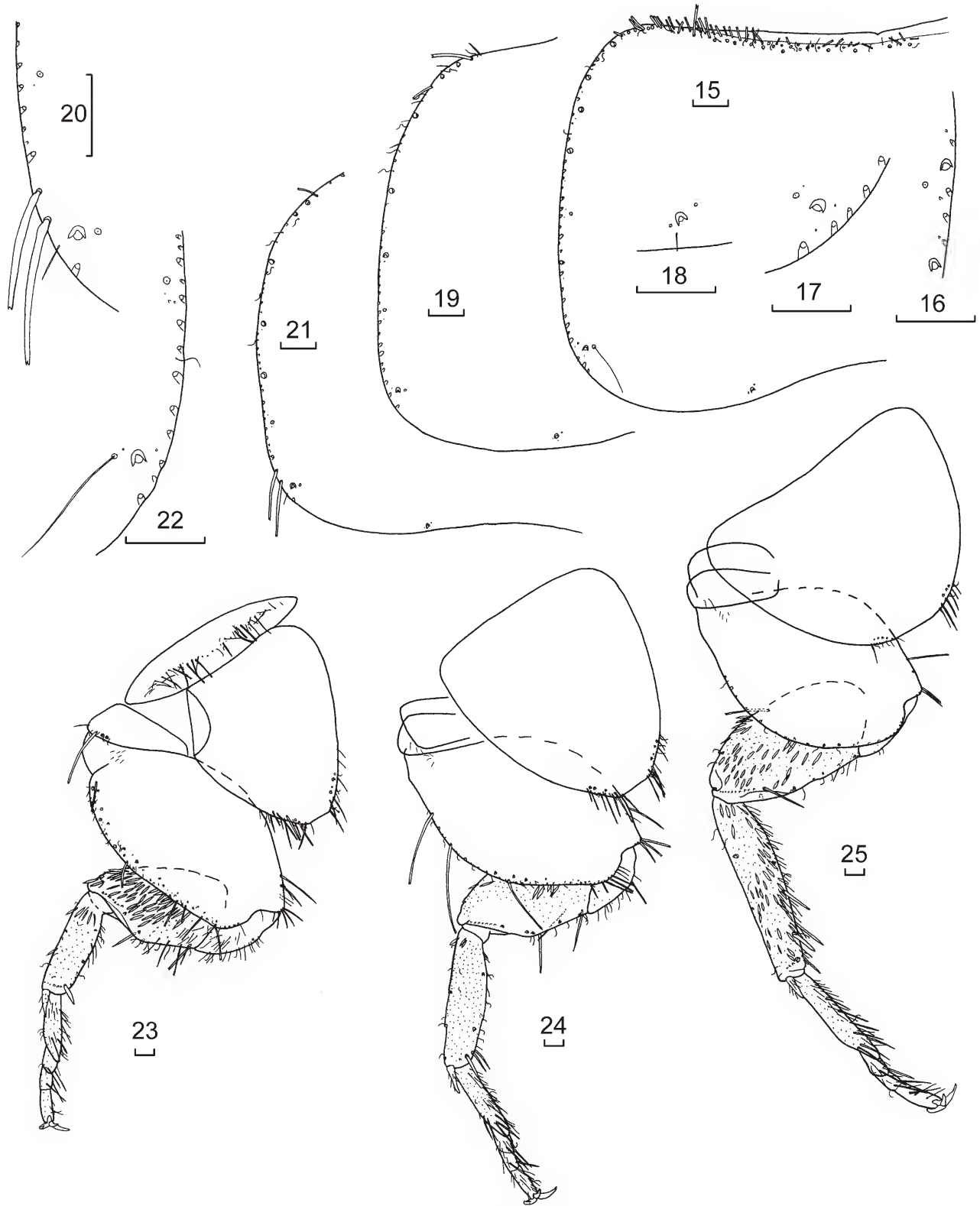
Figure 3. Concatenated 28S and COI 35 taxa only—MrBayes. * Single asterisk indicates paratype, double asterisk is holotype.



Figures 4–14. *Heterolepisma howense* Womersley specimen K.541011 K.541012 ♂ unless otherwise indicated by specimen number (4) dorsal scale; (5) lanceolate scale from femur; (6) head of paratype K.261040; (7) antenna, pedicel and basal intervals of flagellum; (8) idem, proximal four annuli of most distal surviving interval showing location of basiconic sensillum type B (**bsB**); (9) mandible; (10) idem, incisor and molar regions; (11) maxilla, only more prominent setae of palp illustrated; (12) idem, lacinia; (13) idem, apex of ultimate article of palp with its branched papillae (**bp**); (14) labium. Scale bars = 0.1 mm.

Head: Wider than long (Fig. 6), without distinct bushes. Anterior margin of frons glabrous with small medial indented region, lateral margins anteriorly with a single row of strong macrochaetae which becomes about two macrochaetae wide near the anterior margin of the antenna; peri-antennal groups of three larger macrochaetae and several small setae or cilia; the marginal rows continue back to the level of the eyes and a single row of strong macrochaetae extend back above the eyes. Clypeus with numerous setae and cilia, the setae being longer and stronger in the proximal lateral parts, where lanceolate scales also occur. Labrum with several setae scattered over the proximal third and a row of

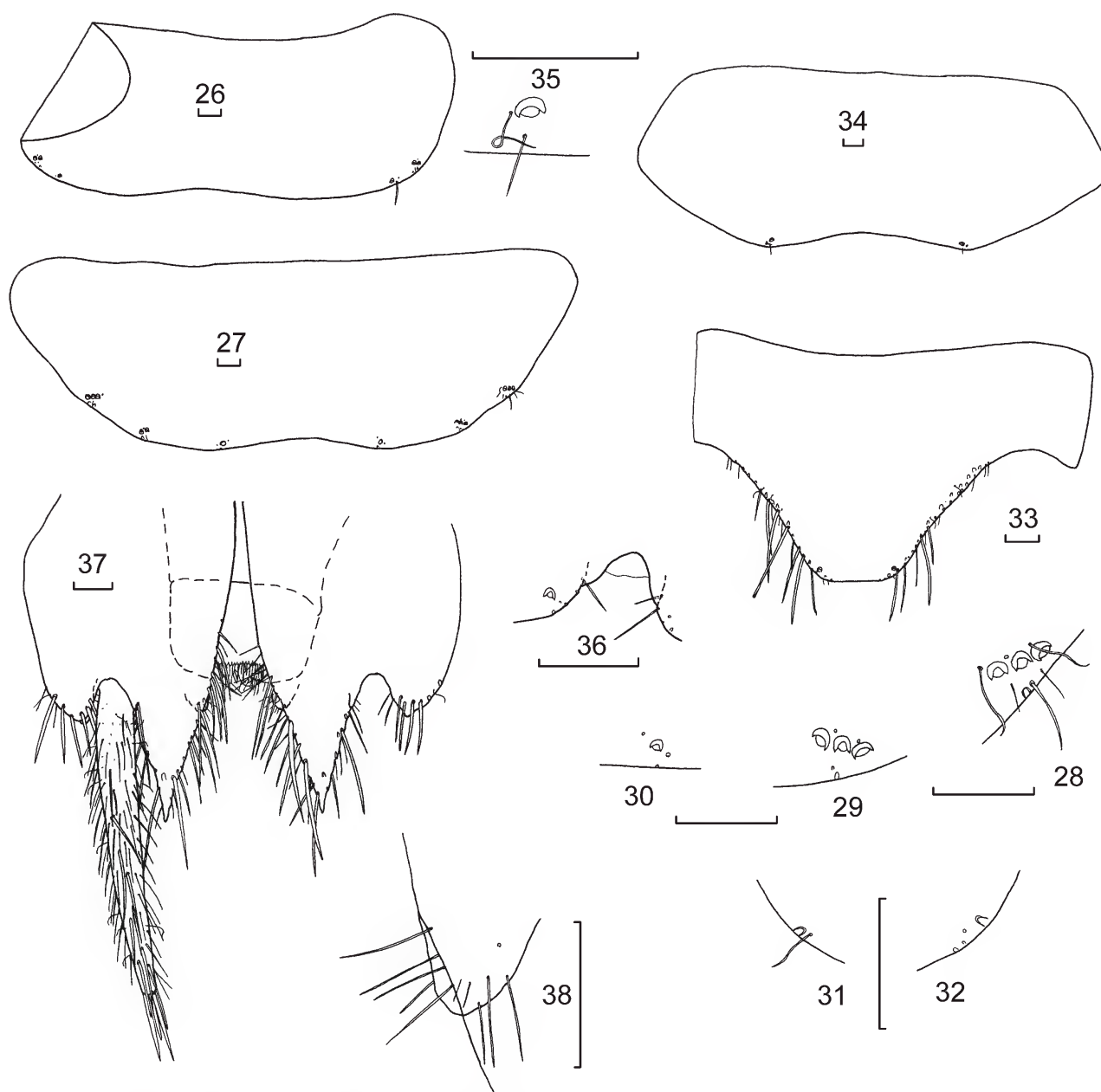
six fine setae medially near the distal margin. — Antennae with scape much longer than pedicel (Fig. 7), scape with a subapical rosette of strong setae, the sides and ventral face with numerous smaller setae and probably some lanceolate scales; pedicel also with subapical rosette of strong setae but also several cilia and small setae in a row proximal to the larger setae. First annulus of flagellum with a subapical ring of setae and some short trichobothria; subsequent annuli similar but becoming slightly longer, dividing into two annuli by the eighth interval and into four annuli by the about the twelfth interval. Most distal surviving intervals of almost complete antenna (Fig. 8) divided into repeated



Figures 15–25. *Heterolepisma howense* Womersley specimen K.541011 ♂ unless otherwise indicated by specimen number (15) pronotum, anterior and left margins; (16) idem, right anterior trichobothrial area; (17) idem, right posterior trichobothrial area; (18) idem, right posterior comb; (19) mesonotum, left side; (20) idem, trichobothrial areas, left side; (21) metanotum, right side; (22) idem, trichobothrial areas, right side; (23) presternum, prothoracic sternum and PI; (24) mesothoracic sternum and PII; (25) metathoracic sternum and PIII. Scale bars = 0.1 mm.

patterns of eight annuli, each with two rosettes of fine setae; rod-like basiconic sensilla (Type B of Adel, 1984) present distally in the distal annulus of each interval. — Mandibles (Figs 9, 10) typical for Heterolepismatinae with well-

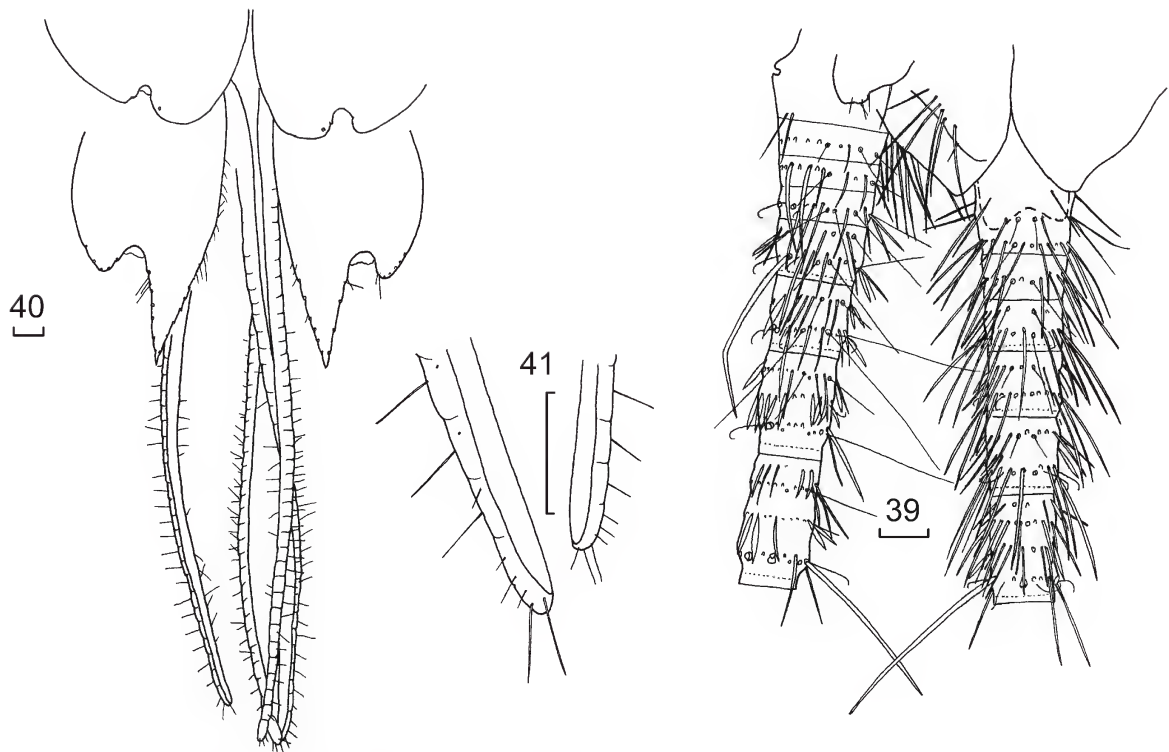
developed molar and incisor areas; a group of about 9–12 strong and short or thin and longer, apically bifurcated setae distally adjacent to the molar region and a bush of about 40 macrochaetae externally. — Maxilla (Fig. 11) with two



Figures 26–38. *Heterolepisma howense* Womersley specimen K.541012 ♂ (26) urotergite I; (27) urotergite IV; (28) idem, right lateral comb; (29) idem, right sublateral lateral comb; (30) idem, right submedial comb; (31) urotergite IX, left infralateral comb; (32) urotergite IX, right infralateral comb; (33) urotergite X; (34) urosternite IV; (35) idem, right comb; (36) urosternite VIII, left stylus insertion; (37) urosternite IX, stylus and penis; (38) left paramere. Scale bars = 0.1 mm.

thick apically bifurcate macrochaetae externally proximal to the palp; lacinia typical for genus, with three strong teeth, one set further back than the other two, followed by about seven lamellate processes and a row of eight or nine thin setae, galea with one slightly stronger seta proximally but otherwise with only short fine cilia or setulae (Fig. 12); apical article of maxillary palp (Fig. 13) 4.1 times longer than wide (range 3.7–4.6) and 1.2 times longer than the penultimate article (range 1.1–1.4), the ultimate article apparently with three (or four on K.541011) branched papillae, ultimate and penultimate articles with fine setae only, third article with subapical rosette of somewhat stronger setae one of which is quite strong, second article with subapical rosette of stronger setae as well as several somewhat stronger setae

on the ventral face, basal articles with rosette of short thicker setae. — Labium (Fig. 14) wider than long, postmentum with setae scattered irregularly across the anterior third and a group of setae in the posterior corners, three or four of which may be quite robust, prementum with transverse and oblique groups of stronger setae and with short setulae distally; apical article of labial palp almost as wide as long (L/W 0.8–1.1) with five compact papillae of similar size arranged in a broad three plus two arrangement, outer margin with one basiconic sensillum (type C) and at least one basiconic sensillum (type B); covered with numerous fine short setae, those proximal and medial longer than those distal and/or lateral; penultimate article without particularly stronger setae.



Figures 39–41. *Heterolepisma howense* Womersley paratype ♀ K.261041 unless otherwise indicated by specimen number (39) base of cerci and medial dorsal appendage ♂ K.541012; (40) coxites VIII and IX and ovipositor; (41) apex of ovipositor valves. Scale bars = 0.1 mm.

Thorax: Pronotum (Fig. 15) with setal collar of short macrochaetae, some small setulae and longer cilia; macrochaetae and setae of lateral margins of Lord Howe Island specimens lost, but the specimen from Norfolk Island (K.261293, K.261294) (see below) has several quite long macrochaetae along the margins of all nota, as well as setulae and long cilia; all macrochaetae are single. Anterior trichobothrium about half way along the margin and not associated with any macrochaeta (Fig. 16). The posterior trichobothrium mediad of a large submarginal macrochaeta (Fig. 17). Both trichobothria with two or three setulae posterior to them. Posterior margin with 1+1 single macrochaetae each associated with two cilia (Fig. 18). — Mesonotum (Figs 19, 20) with similar lateral chaetotaxy to pronotum except there are many more setulae along the margins; the anterior trichobothrial area not associated with any macrochaetae and about $\frac{3}{4}$ the distance along the margin, the posterior area as in the pronotum; 1+1 posterior macrochaetae as in pronotum. — Metanotum (Figs 21, 22) similar to mesonotum (the macrochaeta is missing from the right posterior trichobothrial area of K.541011 but present on all other specimens).

Presternum narrow, with transverse row of strong macrochaetae, setae and cilia (Fig. 23). All thoracic sterna with hyaline scales. — Prothoracic sternum (Fig. 23) parabolic, about as long as wide at its base ($L/W = 0.99$, range 0.85–1.10), posterior one third of lateral margins with marginal setae, 1+1 submarginal combs each of three or four macrochaetae; apex between the combs straight and glabrous with scales extending beyond the margin. — Mesosternum (Figs 24) a little longer than wide ($L/W 1.07$, range 1.04–1.11), similar to prosternum with straight or slightly concave distal glabrous region between the setae, with 1+1 submarginal combs of about five macrochaetae

as well as some strong marginal setae, some cilia and one or two setulae along the posterior fifth of the margin. — Metasternum (Fig. 25) apically rounded, much wider than long ($L/W 0.72$, range 0.69–0.75), with submarginal rows of four or five macrochaetae as well as some marginal setae (some of which are quite robust) and cilia in the posterolateral corners; the gap between the combs about six times the average length of each comb (range 4.7–7.8).

Legs (Figs 23–25) becoming progressively longer and more slender (length tibia PII/PI 1.10–1.34; tibia PIII/PI 1.56–1.98), tibia L/W ratio of legs PI 3.0 (range 2.5–3.6), PII 3.5, (range 3.1–4.5), PIII 4.4 (range 3.3–5.3); tarsi L/W ratio PI 6.0 (range 5.2–6.6), PII 7.9 (range 6.9–8.9), PIII 10.1 (range 8.9–11.3). Precoxa of PI with lateral comb of three strong macrochaetae. Coxa of PI with strong macrochaetae in about two rows along the external margin; inner margin with about five stout macrochaetae distally over the articulation and another two strong longer setae subdistally near long thin setae on the dorsal face. Trochanter with several fine setae as well as one stronger seta. Femur ventrally with several macrochaetae along the posterior margin and another about two thirds the distance along the anterior margin, distal anterior corner with two apically bifurcate macrochaetae, most of ventral face and anterior margin covered with lanceolate scales with setae restricted to the proximal posterior quarter. Tibia with a very strong carrot-shaped macrochaeta distally as well as a few smaller strong setae along the ventral margin, dorsal or outer margin with one or two macrochaetae about midway along the margin and another usually about $\frac{3}{4}$ the distance along the margin; apical spur large and distinctly hooked and bearing a few small setae; ventral face of tibia mostly covered with lanceolate scales. Tarsi of four articles, the basal tarsal article of PI about equal in length to the remaining articles together,

Table 3. Number of macrochaetae per bristle comb—*Heterolepisma howense* Womersley.

segment	urotergite			urosternite
	lateral	sublateral	submedial	lateral
I	2	1	—	—
II	2	2	1	1
III	2–3	2	1	1
IV	3	2–3	1	1
V	3–4	2–3	1	1
VI	3–4	3	1	1
VII	3–4	2–3	1	1
VIII	2–3	—	1	1

bearing some stronger setae below; second and third articles short and subequal, suture between third and fourth articles weak. Pretarsus with two long curved lateral claws and a much shorter straight medial claw. PII (Fig. 24) and PIII (Fig. 25) similar to PI except lacking comb on the precoxal. The relative length of the basal tarsal article is progressively only a little longer, being about 56% of the total length on PIII.

Abdomen: Urotergite I (Fig. 26) with 2+2 small combs, each lateral comb of two macrochaetae associated with a cilium, two small marginal setae and a setula, each sublateral comb of a single macrochaeta associated with a cilium and a small but stout marginal seta; urotergites II–VII with 3+3 combs (Figs 27–30) as shown in table 3, each lateral comb associated with 2–3 cilia, 1–2 marginal setae and 0–3 setulae, each submedial comb associated with 1–3 cilia, 1–2 marginal setae and 0–2 setulae, each submedial comb of a single macrochaeta associated with two cilia and 0–1 setulae; urotergite VIII with 2+2 combs similar to those on the preceding segments, lacking the sublateral comb; urotergite IX (Figs 31, 32) without combs but with 1–2 marginal setae, a cilium and 0–2 setulae in each infralateral corner. Urotergite X (Fig. 33) straight and glabrous across the posterior margin, L/W 0.38–0.48, with 1+1 stronger macrochaetae in each posterolateral corner and several strong macrochaetae some cilia and setulae along most of each lateral margin.

Urosternite I glabrous, urosternites II–VIII with 1+1 lateral combs each of a single macrochaeta each associated with a cilium laterad and posterior to the macrochaeta and usually with a setula closer to the margin (Figs 34–36). Slender styli

present on VIII and IX in male and VII to IX in female; each stylus with several robust macrochaetae apically. Styli IX (Fig. 37) (excluding the apical macrochaetae) a little more than two times the length of the internal process.

Coxite IX of male IX (Fig. 37) similar to female, inner process 3.1–3.4 times longer than outer process (2.5–2.8 times on K.261294 from Norfolk Island), and 1.4 times longer than wide at its base (1.1–1.2 times on K.261294 from Norfolk Island), bearing short parameres which have several short thin setae distributed over their surface (Fig. 38). Penis typical (Fig. 37) with numerous glandular setae apically, each set on a protuberance.

Coxite IX of ♀ (Fig. 40), the internal process acute apically, about four times longer than the external process (range 3.8–4.3) and 1.7 times (range 1.7–1.8) longer than wide at its base, external and internal margins of internal process and external margin of outer process round with a few moderately strong insertions. — Ovipositor long about twice HW (range 1.7–2.3) surpassing the end of the inner process of coxite IX by about three times the length of the inner process, composed of about 40 divisions (range 34–42) and surpassing the apices of styli IX by about the length of the stylus on the specimen from Norfolk Island (K.261292). Distal divisions of gonapophyses (Fig. 41) with only short fine setae and setulae.

Cerci (Figs 39) with four basal divisions shorter than wide then progressively longer with a single rosette of setae, macrochaetae and trichobothria becoming increasingly stronger and longer distally, fifth and sixth divisions with two rosettes, the more proximal with short trichobothria, smaller

Table 4. Selected measurement ratios showing a difference between *Heterolepisma cooloola* and *H. howense*. Number of specimens within parentheses.

measurement parameter	<i>H. cooloola</i> Smith <i>et al.</i> Cooloola		<i>H. howense</i> Womersley Lord Howe Island	
	mean	range	mean	range
prothorax width/HW	1.57 (11)	1.48–1.70	1.40 (7)	1.28–1.45
mesothorax width/HW	1.60 (11)	1.54–1.72	1.44 (7)	1.40–1.49
metathorax width/HW	1.51 (11)	1.40–1.57	1.39 (7)	1.33–1.45
thorax length/abdomen length	0.45 (11)	0.39–0.54	0.56 (7)	0.48–0.75
H+B/HW	7.40 (11)	6.69–8.25	6.25 (7)	5.42–6.57
ultimate max. palp article/HW	0.22 (11)	0.20–0.25	0.27 (5)	0.25–0.29
pedicel/HW	0.07 (9)	0.05–0.09	0.10 (3)	0.09–0.11
urotergite X (L/W)	0.61 (5)	0.54–0.70	0.43 (5)	0.38–0.48
coxite IX inner process (L/W) ♂	1.81 (2)	1.70–1.93	1.30 (2)	1.08–1.38

seta and what appear to be lanceolate scales, macrochaetae restricted to the most distal rosette; seventh division with three rosettes, the probable lanceolate scales restricted to the two basal rosettes; eighth division with four rosettes, the apparent lanceolate scales restricted to the first and third rosettes; eleventh division with eight rosettes, apparent lanceolate scales possibly restricted to the most basal rosette. — Median dorsal appendage (Fig. 39) as illustrated.

Habitat. The type series was collected under bark of “Kilinoque” trees. Other LHI specimens were collected from a rotting log and the Norfolk Island specimen was collected by beating a dead branch. Presumably this species lives under bark or within other cavities on trees.

Remarks

Contrary to earlier opinion (e.g., Smith, 2014), *H. howense* is not a close relative of *H. sclerophyllum* regardless of its similar arrangement of styli, a character which should no longer be considered as a strong indicator of relationship. A specimen from Lord Howe Island mentioned by Smith, 2014 (K.261088 K.261089) has now been shown to belong to *H. milledgei* sp. nov. described below.

Heterolepisma howense appears to be closer to *H. cooloola* from the southern Queensland coastal forests, with which it shares the glabrous anterior margin to the frons, lanceolate scales on the femora and tibia and the arrangement of styli. Unpublished molecular data indicate there are several, as yet undescribed, species in the *cooloola* group along the eastern seaboard of Queensland suggesting north-eastern Australia may have been the origin of the colonising ancestor.

In addition to the characters given in the diagnosis to distinguish this species from *H. cooloola*, morphometric analysis also identified several measurements as potentially useful to separate the species, i.e. very little or no overlap in the range of measurements. These data need to be expanded to include more specimens from a wider geographical spread.

No consistent morphological difference could be found between the specimens collected on Norfolk Island and Lord Howe Island. It is also possible that the presence of this species on both islands (almost 900 km apart) is due to the activities of man. Ships regularly sailed between these islands in the 1800s (e.g., Nicholls, 2006) and possibly even earlier (Anderson and White, 2001). If they were carrying wood collected on one or other island (e.g., as firewood) then silverfish may have been transported along with it. *Heterolepisma howense* may have been a Norfolk Island endemic or vice versa.

Heterolepisma milledgei sp. nov.

<http://zoobank.org/NomenclaturalActs/56C9A2EC-9AEE-449F-8D69-9DAA8A6C0A3C>

Figs 42–85

Holotype. ♂ (HW 1.43) (AM K.541007 K.541008 on two slides) LORD HOWE ISLAND: Stevens Reserve 31.52°S 159.07°E 15m asl, 25.ii.2001, Graham Milledge. **Paratypes.** 1♂ (HW 1.25) (K.377823 in alcohol) same data as holotype; 1♀ (HW 1.03) (K.261088 K.261089 on two slides) LORD HOWE ISLAND: eastern slope of Phillip Point (north head) 31.522°S 159.041°E, 1.xii.2000, CBCR Australian Museum; 1♀ (HW 1.18) (K.261256 K.261257 on two slides) LORD HOWE ISLAND: Blackburn Island 31.534°S 159.060°E,

18.ii.2017, C. Reid; 1♂ (HW 1.25) (K.541013 K.541014 on two slides) LORD HOWE ISLAND: Junction of Kim's Lookout trail and North Beach trail 31.519°S 159.050°E, 18–27.ii.2001, LHI010/04; 1♀ (HW 1.10) (K.377863 (shared) in alcohol) LORD HOWE ISLAND: Western slope of Malabar Ridge S. of Kims Trail, 31.516°S 159.059°E, 24 November 2000, LHI007/L; 1 juvenile (HW 0.75) (K.377863 (shared) in alcohol) same data as previous; 1 juvenile (HW 0.73) (K.377864 in alcohol) LORD HOWE ISLAND: Eastern slope of Dawson's Point ridge near top, 31.516°S 159.049°E, 24.xi.2000, LHI008/L; 1♀ (HW 1.28) (K.377866 in alcohol) LORD HOWE ISLAND: Western slope of Dawson's Point Ridge, off North Beach trail, 31.083°S 159.048°E, 24.xi–1.xii.2000, LHI12/03; 1 partial specimen (HW 1.18) (K.377867 (shared) in alcohol) LORD HOWE ISLAND: Junction of Kim's Lookout trail and North Beach trail, S31.519° E159.050°, 18–27.ii.2001, LHI010/02, (head, thorax and abdominal segments I–III); 1 partial specimen (HW 0.93) (K.377867 (shared) in alcohol) same data as previous, (head, thorax and abdominal segments I–V); 1♂ (HW 0.95) K.261258 on one slide) LORD HOWE ISLAND: Balls Pyramid, base of “Pillars of Porteus” 31.757°S 159.255°E, 26.iii.2017, F. Koehler (specimen probably subadult as styli VIII are only about half the expected size); 1 juvenile ♂ (HW 0.68) (K.261349 on one slide) LORD HOWE ISLAND: Balls Pyramid, rock platform at southern tip “Base Camp” 31.7575°S 159.2550°E, 26.iii.2017, F. Koehler; 1 juvenile ♂ (HW 0.73) (K.377869 in 100% ethanol), same data as previous; 1 juvenile ♀ (HW 0.70) (K.377827 in 80% ethanol) same data as previous; 1 juvenile (HW 0.63) (K.377870 in 100% ethanol) same data as previous.

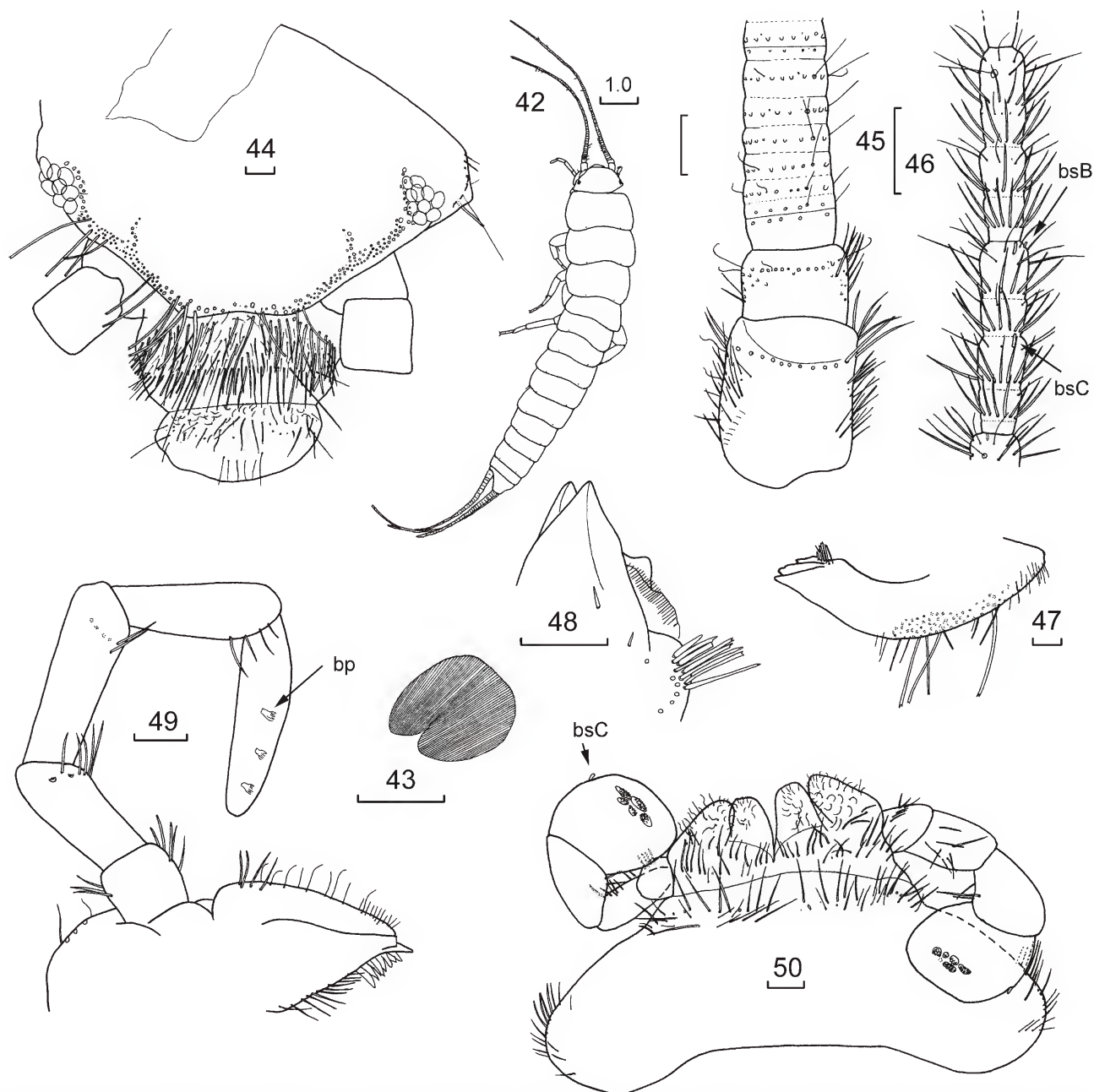
Diagnosis. This species can be distinguished from most other described species of *Heterolepisma* by a combination of features including the presence of macrochaetae along the anterior margin of the frons, the absence of a medial comb on urosternite I, the presence of only 1+1 macrochaetae on urosternites II–VIII and the number of styli (three pairs in the ♀ and two pairs in the ♂). It differs from the closely related *H. sclerophyllum* species group most obviously in the shorter urotergite X (L/W at its base of 0.36–0.47 vs 0.43–0.73) and its truncate trapezoidal shape (versus rounded).

Description

Appearance: Medium sized silverfish (Fig. 42), thorax about 15% wider than abdomen which only tapers slightly posteriorly from about the fifth abdominal segment; appearance when live unknown.

Body length: H+B 10.1 mm; HW 1.43 mm; thorax: length up to 3.2 mm or 0.31 H+B (range 0.29–0.32); width up to 2.13 mm with no great difference in length or width between the nota although the mesonotum is the widest and the pronotum the narrowest; antennae not complete >5.2 mm or >0.54 H+B; terminal filaments all damaged, >4.0 mm or >0.43 H+B.

Pigmentation: Pigment brownish, quite variable between specimens, with the specimen from Blackburn Island being much darker than the holotype, while others show intermediate levels of pigmentation, the variability perhaps due to the maturity of the specimen and the duration in alcohol. Flagellum of antennae evenly pale becoming slightly darker distally; pedicel and scape without pigment. Terminal



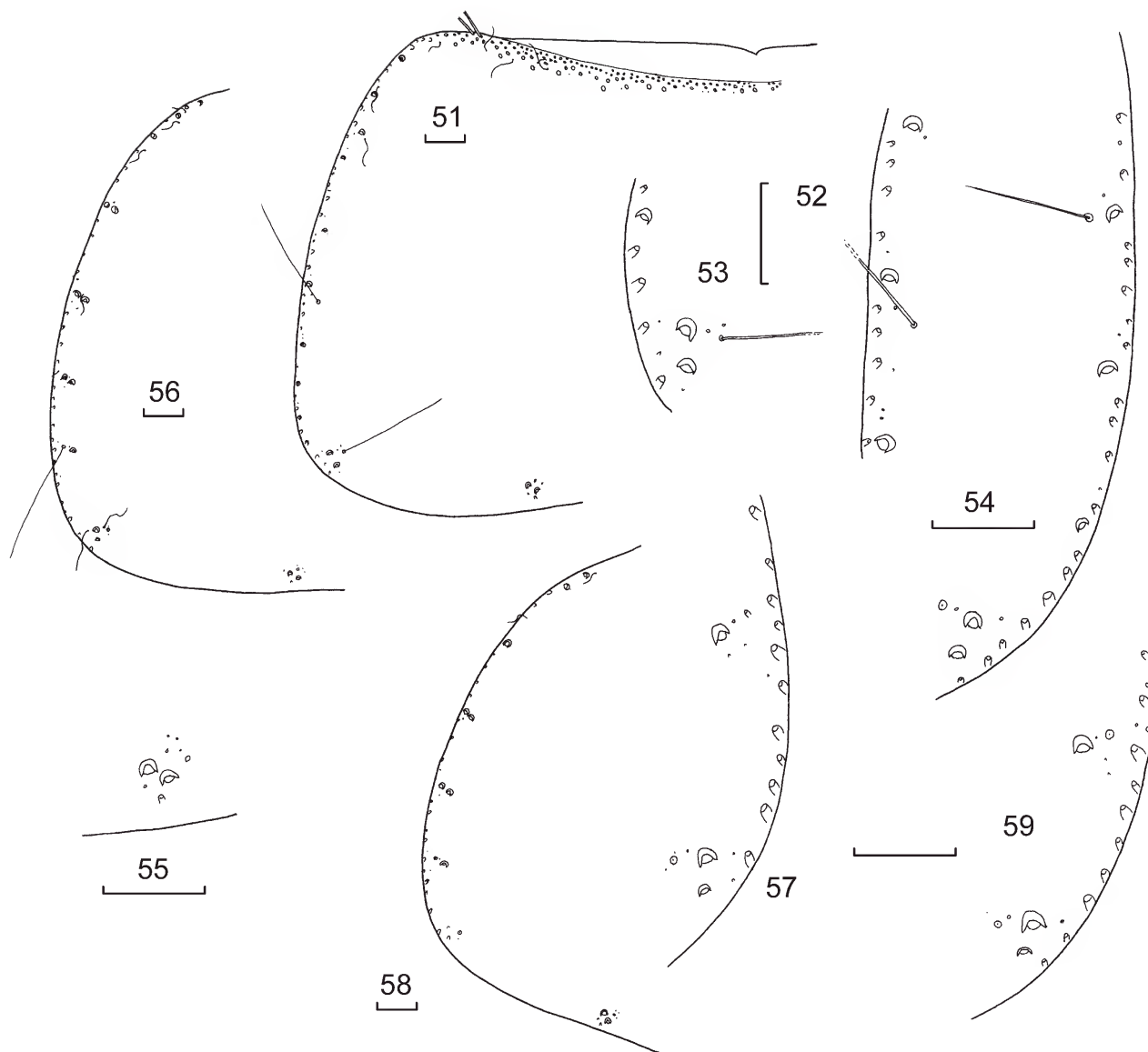
Figures 42–50. *Heterolepisma milledgei* sp. nov. holotype ♂ specimen K.541007 K.541008 unless otherwise indicated by specimen number (42) habitus K.377823; (43) scale from urotergite II; (44) head; (45) antenna, scape, pedicel and basal intervals of flagellum; (46) idem, most distal surviving interval showing basiconic sensillum type B (**bsB**) and type C (**bsC**); (47) mandible; (48) idem, incisor and molar regions; (49) maxilla, ultimate article of palp with its three branched papillae (**bp**), only more prominent setae of palp illustrated; (50) labium, only more prominent setae of palp illustrated, basiconic sensillum type C indicated (**bsC**). Scale bars = 0.1 mm unless otherwise indicated.

filaments annulated darker brown with only the most distal part of each major division from just below the rosette of major macrochaetae to the suture with the next division devoid of pigment. Head with very small area of pigment around eyes only. Clypeus, labrum and mandibles without pigment. Maxillary palp without pigment except for slightly shaded penultimate article. Labium and labial palp largely without pigment except for small amount along the outer margin of the penultimate article. Legs without pigment except for dorsal face of the tibia and the first tarsal article of PIII where light pigment is fairly evenly distributed and a small amount on the tibia distally of PII. Urotergite X with light pigment, darkest proximally and becoming lighter distally. Coxites IX around stylus insertion and both pair of

styli with very dark pigment in one specimen (K.541014), only styli IX pigmented in another specimen (K.541014), weaker in the holotype and almost absent in K.261258. Ovipositor without pigment.

Macrochaetae: Typical for the Heterolepismatinae, smooth, hyaline or slightly straw coloured, apically bifurcate with truncated tips to each bifurcation. Some macrochaetae on tibia, stout carrot-shaped.

Scales: Quite broad, hyaline or with ribs browner distally, with numerous subparallel ribs that do not surpass the margin of the scale (Fig. 43). Scales found on top of head, absent from clypeus and labrum as well as all cephalic appendages; present on all nota, all thoracic sterna, and coxae of legs but

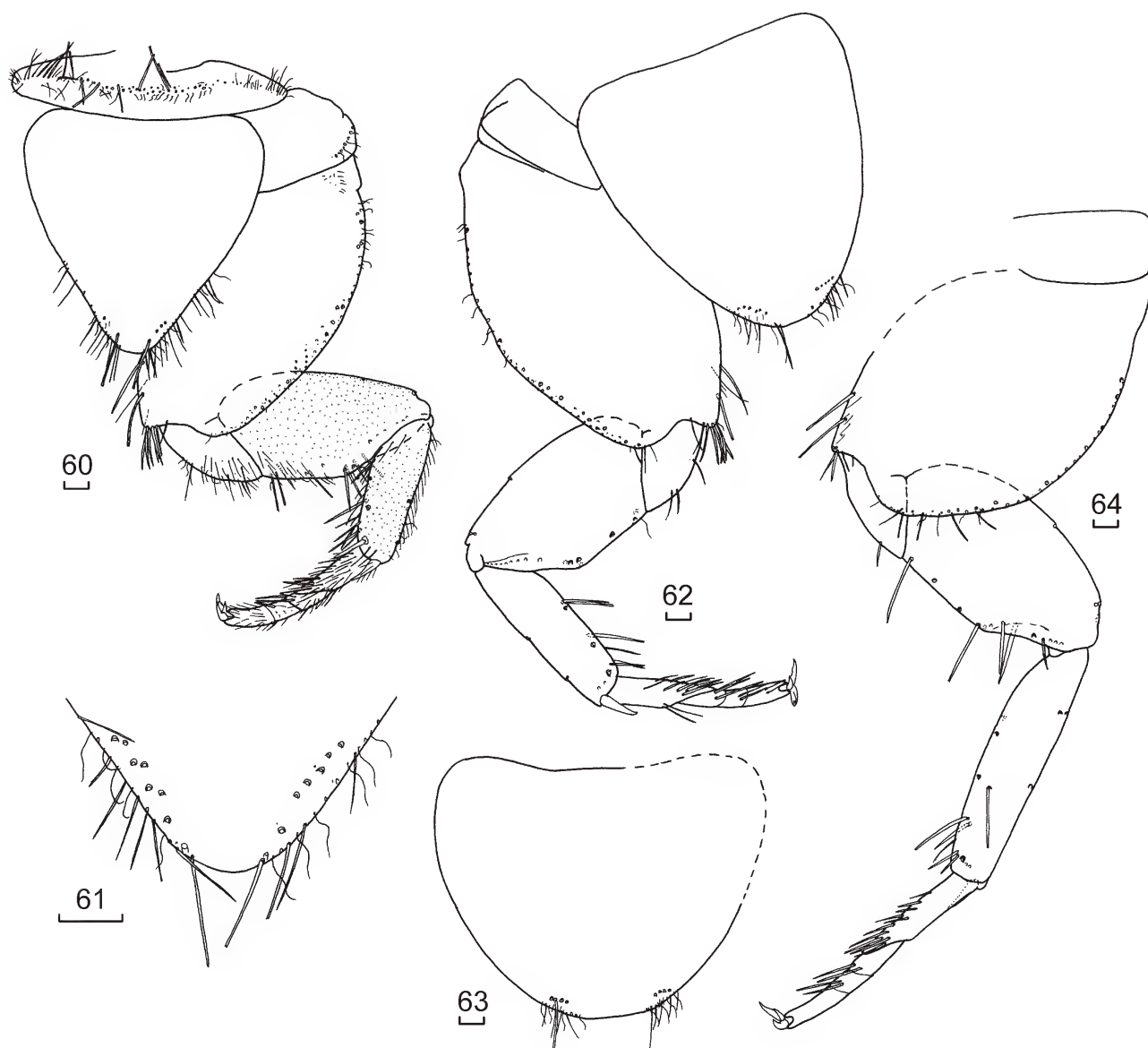


Figures 51–59. *Heterolepisma milledgei* sp. nov. holotype ♂ specimen K.541007 K.541008 (51) pronotum, anterior and left margins; (52) idem, left anterior trichobothrial area; (53) idem, left posterior trichobothrial area; (54) idem, posterior half of right margin; (55) idem, left posterior comb; (56) mesonotum, left side; (57) idem, trichobothrial areas, right side; (58) metanotum, left side; (59) idem, trichobothrial areas, right side. Scale bars = 0.1 mm.

absent from remaining leg articles, present on all urotergites and urosternites, absent from styli and terminal filaments. Lanceolate scales not seen.

Head: Wider than long (Fig. 44). Frons with complete row of strong macrochaetae along the anterior margin which join laterally with the rows of macrochaetae along the lateral margins, running back towards and above the eyes, these rows quite dense about 2–4 macrochaetae wide, peri-antennal groups of about six macrochaetae and smaller setae, contiguous with the lateral marginal row. Clypeus with 1+1 long rows of macrochaetae (ca. seven or more in adult specimens) proximally and another transverse row of thinner but still well-developed setae a little distal of the middle, two of these setae on each side are long, trichobothria-like; area between these two rows well populated with setae, many of which are quite long. Labrum with transverse proximal band of cilia followed by a band of setae in proximal half, distal half with the usual row of six fine setae. — Antennae with scape longer than pedicel (Fig. 45), each with a subapical

rosette of small macrochaetae and setae, as well as some cilia; ventral and lateral faces of scape, and to a lesser extent also the pedicel, with many setae and some cilia. First annulus or interval of flagellum with a subapical rosette of a few setae; subsequent six annuli with a single rosette of small setae, trichobothria and some cilia, the sutures between the annuli difficult to see in the holotype, eighth to tenth intervals divided into two annuli, each with a rosette similar to the previous, eleventh and twelfth intervals divided into two annuli but the apical annulus has two rosettes, following interval still divided into two annuli but each has two rosettes, the most distal surviving interval in the holotype (probably about mid-antenna) with four annuli per interval, each with two rosettes, the trichobothria restricted to the most distal rosette, in paratype K.261256 the antenna is much more intact (three quarters?), each apical interval is divided into eight annuli with trichobothria still restricted to the most distal annulus, with a small basiconic sensillum (type B) at least on the fourth annulus of each interval and possibly

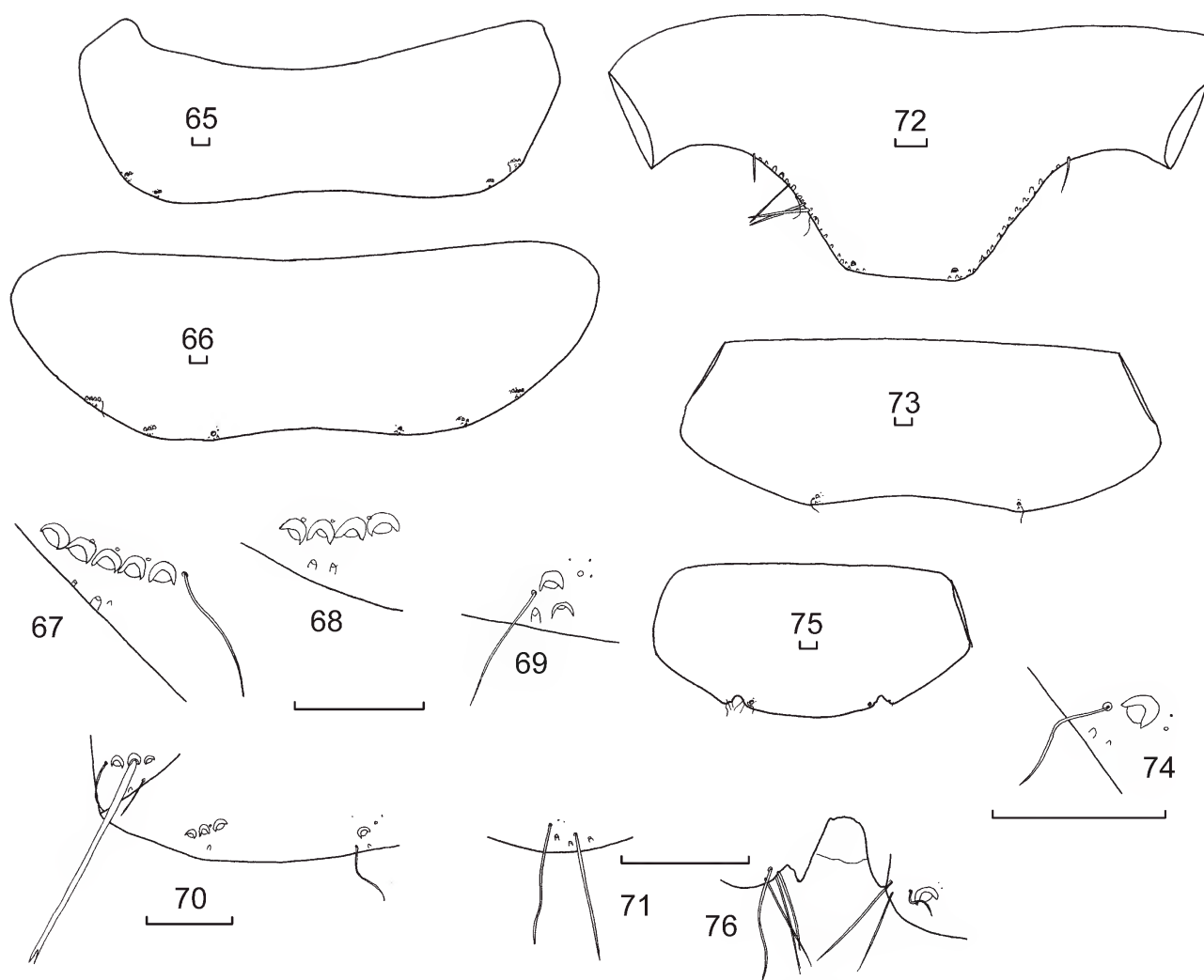


Figures 60–64. *Heterolepisma milledgei* sp. nov. holotype ♂ specimen K.541007 K.541008 unless otherwise indicated by specimen number (60) presternum, prothoracic sternum and PI; (61) prothoracic sternum of K.541013; (62) mesothoracic sternum and PII; (63) metathoracic sternum; (64) PIII. Scale bars = 0.1 mm.

also on the most distal annulus, as well as two basiconic sensilla type C, one on the second and the other on the fourth annulus (Fig. 46). — Mandibles (Figs 47, 48) typical for Heterolepismatinae with well-developed molar and incisor areas, a group of about 7–15 short apically bifurcated setae distally adjacent to the molar region and a bush of about 50–60 long macrochaetae externally. — Maxilla (Fig. 49) with three thick apically bifurcate macrochaetae externally proximal to the palp; lacinia short and wide, with three strong teeth, one set further back than the other two, followed by about seven lamellate processes and a row of 7–11 setae, galea with 0–5 stronger setae proximally but otherwise with only short fine cilia or setulae; apical article of maxillary palp 4.6 times longer than wide (range 4.3–4.7) and 1.3 times longer than the penultimate article (range 1.1–1.5), the ultimate article with three branched papillae, those in the male larger and more elaborate than those in the female; all articles of palp covered with fine setae, penultimate article with a few somewhat stronger setae subapically, first, second and

third articles with incomplete subapical rosettes of stronger setae. — Labium (Fig. 50) wider than long, postmentum with several quite strong setae in each posterolateral corner, quite long simple setae in band about two wide across the anterior quarter, prementum with transverse and oblique groups of strong often slightly apically bifurcate setae and with short setulae distally; apical article of labial palp, 1.2 times longer than wide (range L/W 1.1–1.3) with five papillae arranged in a cluster arrangement with the three larger papillae in a curved line around the posterior two smaller papillae; outer margin with at least two basiconic sensilla (one type C, one type B); penultimate article with three stronger setae medially, second article with several stronger setae on the inner face and subdistally, basal article with several short strong setae in an oblique line on the anterior face.

Thorax: Pronotum (Fig. 51) with well-developed setal collar about three or four macrochaetae wide and some long cilia scattered throughout collar; chaetotaxy of lateral margins largely lost, consisting of many marginal setae or

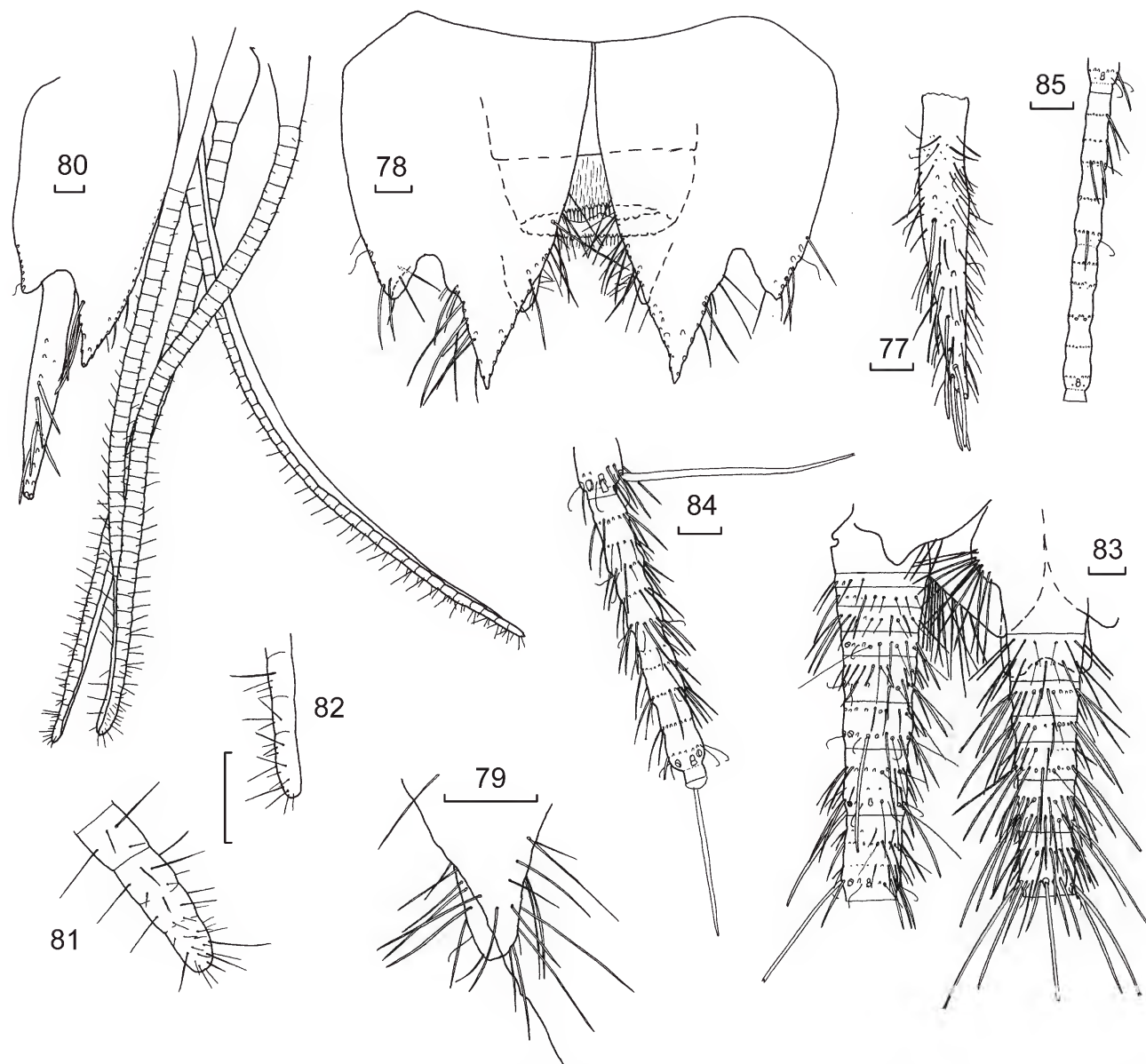


Figures 65–76. *Heterolepisma milledgei* sp. nov. holotype ♂ specimen K.541007 K.541008 unless otherwise indicated by specimen number (65) urotergite I; (66) urotergite III; (67) urotergite V, left lateral comb; (68) idem, left sublateral lateral comb; (69) idem, left submedial comb; (70) left side combs of urotergite VII of K.261258 from Balls Pyramid (urotergite folded over between lateral and sublateral combs); (71) urotergite IX, right infralateral comb; (72) urotergite X; (73) urosternite II; (74) idem, left comb; (75) urosternite VIII of ♂; (76) idem, detail of stylet insertion. Scale bars = 0.1 mm.

macrochaetae as well as several submarginal macrochaetae and long cilia. Anterior trichobothrium a little further than halfway along the margin and occasionally associated with a marginal macrochaeta but more often not, otherwise without any special chaetotaxy other than sometimes a couple of setulae (Fig. 52, 54). The posterior trichobothrium mediad of two submarginal macrochaetae with some two or three setulae and long cilia (Fig. 53, 54). Posterior margin with 1+1 submedian combs of two macrochaetae each associated with one or two setulae perhaps two cilia or setulae anterior to the comb (Fig. 55). — Mesonotum (Fig. 56) with similar lateral chaetotaxy to pronotum except two or three of the submarginal macrochaetae are arranged as combs of two macrochaetae; both trichobothrial areas are more posterior (Fig. 57), the anterior trichobothrium about 80% along the margin and located between a macrochaeta and the margin and the posterior area as in the pronotum, in one example (right side only of K.261088) there are two macrochaetae mediad of the trichobothrium; 2+2 posterior macrochaetae as in pronotum. — Metanotum (Figs 58, 59) similar to mesonotum.

Presternum narrow, with transverse band of strong mostly apically bifurcate macrochaetae one or two wide plus small setae and cilia (Fig. 60). All thoracic sterna with hyaline scales. — Prothoracic sternum (Figs 60, 61) cordiform, about as long as wide at base (L/W range 0.84–1.05), posterior two fifths of lateral margins with long thin setae and cilia, 1+1 quite variable combs of 2–9 macrochaetae subparallel to the margin subdistally. — Mesosternum (Fig. 62) semi-elliptical, a little longer than wide (range L/W 1.02–1.15) with 1+1 subdistal combs of five, six or seven macrochaetae as well as several marginal setae, cilia and setulae. — Metasternum (Fig. 63) apically rounded or straight for a distance between the combs, wider than long (range L/W 0.73–0.76) with 1+1 subapical combs, each of 3–7 macrochaetae, the lateral margins adjacent to each comb with setae, cilia and setulae, the gap between the combs about four times the average width of the combs (range 2.8–4.9).

Legs (Figs 60, 62, 64) becoming progressively longer and more slender (mean tibia length PII/PI 1.3 (range 1.23–1.31), PIII/PI 1.70 (range 1.63–1.75), mean tarsus length PII/PI 1.1



Figures 77–85. *Heterolepisma milledgei* sp. nov. holotype ♂ specimen K.541008 unless otherwise indicated by specimen number (77) stylus IX of ♀ K.261257; (78) coxites IX of ♂, penis and parameres; (79) left paramere; (80) coxite IX of ♀, stylus and gonapophyses K.261257; (81) apex of anterior gonapophysis K.261257; (82) apex of posterior gonapophysis K.261257; (83) base of cerci and medial dorsal appendage; (84) apex of cercus; (85) apex of median appendage. Scale bars = 0.1 mm.

(range 1.00–1.25), PIII/PI 1.50 (range 1.37–1.55), tibia L/W ratio of legs PI 3.1 (range 2.5–3.6), PII 3.6 (range 3.5–3.7), PIII 4.0 (range 3.8–4.2); tarsi L/W ratio PI 6.2 (range 6.1–6.3), PII 6.3 (range 5.9–6.8), PIII 9.2 (range 8.5–9.8). Precoxa of PI with comb of about six macrochaetae. Coxa of PI with combs of one or two macrochaetae in the anterolateral corner, many scattered macrochaetae as well as some cilia and setulae along the outer margin, becoming more numerous distally; inner margin with seven macrochaetae distally over the articulation and another one or two strong macrochaetae subdistally, as well as a seta subdistally and a long thin seta on the dorsal face. Trochanter with several long setae, three or four thicker than the rest. Femur ventrally with several strong macrochaetae along the posterior margin and two subdistally over the articulation, numerous thin setae, some quite long scattered over the ventral and dorsal surfaces. Tibia with a strong carrot-shaped macrochaeta distally as long as apical

spur and another two subequally spaced along the ventral margin, as well as several longer macrochaetae along the entire length of the ventral margin, dorsal or outer margin with one short pointed macrochaeta or two macrochaetae just distad of the middle and another subdistally; surface covered in long fine setae; apical spur bearing several small setae. Tarsi of four articles, the basal tarsal article about as long as the following articles together on PI, PII and PIII; all articles bearing numerous long thin setae, including longer stronger setae on the ventral surfaces, suture between third and fourth articles weak. Pretarsus with two long curved lateral claws and a straight medial claw. PII and PIII similar to PI.

Abdomen: Urotergite I with 2+2 combs, the lateral combs of 2–3 macrochaetae each associated with 1–2 cilia, two marginal setae and two setulae, the sublateral combs of two macrochaetae each associated with 1–2 cilia, a marginal seta and a setula (Fig. 65); urotergites II–VII with 3+3 combs, the

number of macrochaetae per comb is shown in table 5, each lateral comb associated with one to four cilia, two marginal setae and sometimes a setula (Figs 66–70); urotergite VIII with 2+2 combs, lacking the sublateral comb (only one large seta in submedial comb on urosternite VIII in specimen K.541014); urotergite IX without combs but with 0–2 cilia and 2–4 small marginal setae or setulae in each infralateral corner (Fig. 71). Urotergite X (Fig. 72) short, trapezoidal (L/W 0.39, range 0.36–0.47) with glabrous posterior margin between one or two submarginal macrochaetae in the posterolateral corners, lateral margins with several macrochaetae, setae and some cilia along entire length.

Urosternite I glabrous; urosternites II–VII with 1+1 macrochaetae each associated with a cilium laterad of the insertion, a small seta and one or two setulae between the macrochaeta and the margin (Figs 73, 74) (macrochaeta missing on one side of urosternite VII in K.541014 but cilium and seta still present); urosternite VII in female with straight posterior margin and a macrochaeta mediad of each stylus insertion and a cilium laterad of the stylus insertion, and two or three setulae on each side; urosternite VIII in the male entire (Fig. 75), its posterior margin slightly convex, its chaetotaxy similar to urosternite VII in the female (Fig. 76). Three pairs of styli in the females VII–IX (Fig. 77) and two in the male (VIII–IX).

Coxites IX of ♂ with acute inner process about 1.2 times longer than wide at its base (range 1.11–1.24) and about 2.8 times longer than the external process (range 2.63–3.31) reaching to just under half the length of the stylus, both inner and outer processes with several macrochaetae/setae along their margins emerging from both the dorsal and ventral surfaces of the processes close to or on the margin. Parameres (Figs 78, 79) a little longer than wide, with about twenty fine setae and some cilia. Penis typical for genus with numerous glandular setae apically, each set on a protuberance.

Coxite IX of ♀ (Fig. 80), the internal process acute apically, about twice as long as the external process and 1.3 times as long as broad at its base, not reaching to half the length of the stylus; external and internal margins of internal process and external margin and apex of outer process with many moderately strong setae directed both up and down. — Ovipositor (Fig. 80), very long and thin (up to 2.1 HW), surpassing the apex of stylus IX by about the length of the stylus (excluding terminal macrochaetae), composed of 39–42 divisions. Distal divisions of gonapophyses VIII and IX with only short fine setae and setulae (Figs 81, 82).

Cerci (Figs 83, 84) with five basal divisions short with no more than a single rosette of setae and trichobothria,

sixth and seventh divisions each with two rosettes of setae, cilia and trichobothria and macrochaetae in the apical rosette of the seventh, subsequent divisions with three then four rosettes with macrochaetae confined to the most apical division, eight rosettes per divisions from about the thirteenth, the divisions progressively longer; most apical surviving division (about 16th in holotype) with ten rosettes per division. — Median dorsal appendage (Figs 83, 85) with glabrous first division, the following division either has two rosettes or the suture between the rosettes is too faint to see, the following two divisions with a single rosette of setae and trichobothria, the next two divisions with two rosettes and the following divisions with four rosettes; most apical surviving division (about 16th in holotype) with ten rosettes per division (Fig. 85).

Balls Pyramid variant: Both Balls Pyramid specimens dissected and mounted had only one macrochaeta in each submedial comb of the urotergites. While the possibility that this is due to their small size cannot be excluded (HW <1.03), this seems unlikely as the submedial combs of the nota in both specimens have two macrochaetae. It would appear that this could represent a morphological difference between the populations on Lord Howe Island and Balls Pyramid suggesting a fairly long period of separation. Both populations however shared identical 28S sequences and are therefore considered here as belonging to a single species (see discussion below).

Juvenile stages: In the small juvenile ♂ (K.261349) from Balls Pyramid there were no combs of two macrochaetae on the lateral margins of the meso- and metanota and only one pair of styli were developed. These observations are consistent with growth characteristics of the genus.

Habitat. Specimens were reported as collected by fogging a Banyan Fig, in leaf litter in closed rainforest (*Drypetes/Cryptocarya*) or (*Cleistocalyx/Chionanthus*), from litter in broad megaphyllous closed sclerophyll forest- (*Howea belmoryana* habitat), under rocks/logs, beating *Lagunaria/Cassinia*, and in a pitfall trap. This suggests it dwells in leaf litter accumulations, probably in areas either protected from rain or which dry out quickly, as is the case with *H. sclerophyllum*. *Heterolepisma howense* on the other hand seems to live under bark or within other cavities on trees. A similar separation of species has been seen by the first author on the Australian mainland where *H. sclerophyllum* is almost always collected from leaf litter accumulations and only rarely from the bark of trees while a sympatric

Table 5. Number of macrochaetae per bristle comb—*Heterolepisma milledgei* sp. nov. Number of macrochaetae for Balls Pyramid specimens is shown within parentheses.

segment	urotergite			urosternite
	lateral	sublateral	submedial	lateral
I	2–3	2	—	—
II	3 (2)	3 (2–3)	2 (1)	1
III	4 (3)	3–4 (3)	2 (1)	1
IV	3–5 (3)	4 (2)	2 (1)	1
V	4–5 (3)	3–4 (3)	2 (1)	1
VI	4–5 (3)	3–4 (3)	2 (1)	1
VII	4 (3)	3–4 (3)	1–2 (1)	0–1
VIII	3–4	—	2 (1)	1

undescribed species in the *H. highlandi* group was only ever taken from bark.

Etymology. Named for the collector of the type specimen Dr Graham Milledge, an arachnologist at the AMS.

Remarks

This new species is closely related to *H. sclerophyllum*. Comparison of morphometric data failed to find a character (other than the L/W ratio of urotergite X) that clearly separated *H. milledgei* sp. nov. from *H. sclerophyllum*. It is possible that a difference exists in the number of ovipositor divisions (for most genotypes except that of the Megalong genotype) and the ratio of stylus VIII/IX, however data for *H. milledgei* sp. nov. is limited. There also appears to be a difference in the width of the gap between the combs on the metathoracic sternite (3.16–4.92 vs 1.66–3.72) except for the Glenbrook genotype (2.38–4.11). *Heterolepisma milledgei* sp. nov. also appears to have denser setae but an objective measure that encompasses the range of instars and the quality of preservation is currently lacking. The very limited data available suggest that there are fewer setulae in the trichobothrial areas but the number of setulae in the *sclerophyllum* complex needs to be re-examined.

Molecular data presented in Smith et al., 2019 found that distances of 0.9–1.8% or greater in 28S, and 7.2–14% in COI were associated with morphologically distinct species. We were able to obtain similar molecular data (Fig. 3) for three specimens here considered to belong to *H. milledgei* sp. nov., a subadult male and a juvenile from Balls Pyramid and a female from Blackburn Island (a small atoll within the main Lagoon of Lord Howe Island). The distance between *H. milledgei* sp. nov. and *H. sclerophyllum* for the 28S gene was 1.3% and 18.4–25.2% for COI. We consider this degree of difference, associated with a consistent morphological difference (trapezoidal urotergite X) as sufficient for *H. milledgei* sp. nov. to be considered as a species distinct from *H. sclerophyllum*. While distances of 6.9–8.1% were found for the COI gene between the Balls Pyramid and Blackburn Island specimens, as well as a difference in the number of macrochaetae in the submedial combs on the abdominal tergites, the two populations had identical 28S sequences. We therefore consider them to belong to the same species, but the differences in morphology and COI sequences suggest that these two populations have been isolated from each other for some considerable time and that they derived from a progenitor near to or the same as *H. sclerophyllum* from the eastern coast of mainland Australia.

Smith (2014) mentioned a specimen of *H. howense* from Lord Howe Island (K.261088 K.261089) that he compared to the newly described *H. sclerophyllum*. Hardly considering

that there could be two species of *Heterolepisma* on Lord Howe Island he believed, due to the arrangement of styli and the shape of urotergite X, that the specimen belonged to the inadequately described *H. howense*, however, the redescription of *H. howense* above, now makes it clear that this specimen is not *H. howense* but belongs to *H. milledgei* sp. nov..

Heterolepisma pyramidum sp. nov.

<http://zoobank.org/NomenclaturalActs/52FB2021-A86E-49BD-87EA-F77EC0F32755>

Figs 86–126

Holotype. ♀ (HW 1.20) (AM K.261254 K.261255 on two slides) LORD HOWE ISLAND: Balls Pyramid, rock platform at southern tip “Base Camp”, 31.7575°S 159.2550°E, 26.iii.2017, F. Koehler.

Diagnosis. This species can be distinguished from many species of *Heterolepisma* by the absence of macrochaetae along the anterior margin of the frons, by the presence of lanceolate scales on the clypeus, femora, tibia and terminal filaments and the presence of a medial comb on urosternite I. Within the remaining group of several species that definitely have these characters (*H. bisetosum*, *H. parvum*, *H. heraldense* sp. nov. and *H. serranoi*) and others that probably have these characters (*H. exacta*, *H. japonicum*, *H. mossambicense*, *H. primafrum* and *H. rouxi*), *H. pyramidum* sp. nov. can be distinguished from all by a combination of the number of macrochaetae in the posterior combs of the nota (one rather than two), the absence of a macrochaeta associated with the anterior trichobothrial area of the pronotum, the composition of the urosternal combs being of greater than a single macrochaeta, the arrangement of styli (three pair in the ♀ and only two pair in the ♂) and the lesser number of combs on urotergite I (2+2 vs 3+3).

Description

Appearance: Medium sized silverfish, thorax about 15% wider than abdomen which only tapers slightly posteriorly from about the fifth abdominal segment; appearance when live unknown (Fig. 86).

Body length: H+B 8.9 mm; HW 1.20 mm; thorax: length 2.5 mm or 0.28 H+B; width up to 1.85 mm, widest at the mesonotum, pronotum and mesonotum slightly longer than the metanotum; antennae almost complete at 5.3 mm or 0.59 H+B; cerci and median dorsal appendage almost complete at 5.2 mm and 5.9 mm (0.58 and 0.67 H+B) respectively.

Pigmentation: Pigment brownish. Flagellum of antennae evenly light brown becoming slightly darker distally; pedicel

Table 6. Selected measurement ratios showing a difference between *Heterolepisma sclerophyllum* (all genotypes) and *H. milledgei* sp. nov. Number of specimens within parentheses.

	<i>H. sclerophyllum</i> Smith NSW all genotypes		<i>H. milledgei</i> sp. nov. Lord Howe Island and Balls Pyramid	
measurement parameter	mean	range	mean	range
metasternum L gap/L combs	2.68 (44)	1.57–4.11	3.80 (5)	2.84–4.92
urotergite X (L/W)	0.57 (29)	0.43–0.73	0.39 (5)	0.36–0.47
ovipositor divisions (number)	37.3 (17)	32–41	40.2 (2)	39–42

without pigment, scape with small patch of pigment above as well as on its insertion pedestal. Terminal filaments annulated darker brown with only the portion of each major division distad of the rosette of larger macrochaetae unpigmented (e.g., the distal end of every eighth subdivision distally). Head with pigment around eyes and along lateral margins to the level of the perpendicular band of macrochaetae. Maxillary palp with light pigment on distal article, penultimate article and third article with even pigmentation, but much less on the second article. Ultimate article of labial palp with light pigment along lateral margins, penultimate article more pigmented, especially laterally and a small amount of pigment on external margin of second article. Precoxae with pigment and dark scales, coxae with light pigment only along lateral margins, trochanter without pigment, femur with small area of pigment distally on the leading edge as well as along the posterior margin, tibia with pigment over much of surface but darker on the dorsal margin, first tarsal article pigmented. Urotergite X and coxites IX pigmented. Styli IX with light pigment distributed evenly. Ovipositor white or perhaps slightly yellowish.

Macrochaetae: Smooth, hyaline to straw-coloured to moderate brown, apically bifurcate with truncated tips to each bifurcation (Fig. 87). Some macrochaetae on tibia, stout carrot-shaped (Fig. 88).

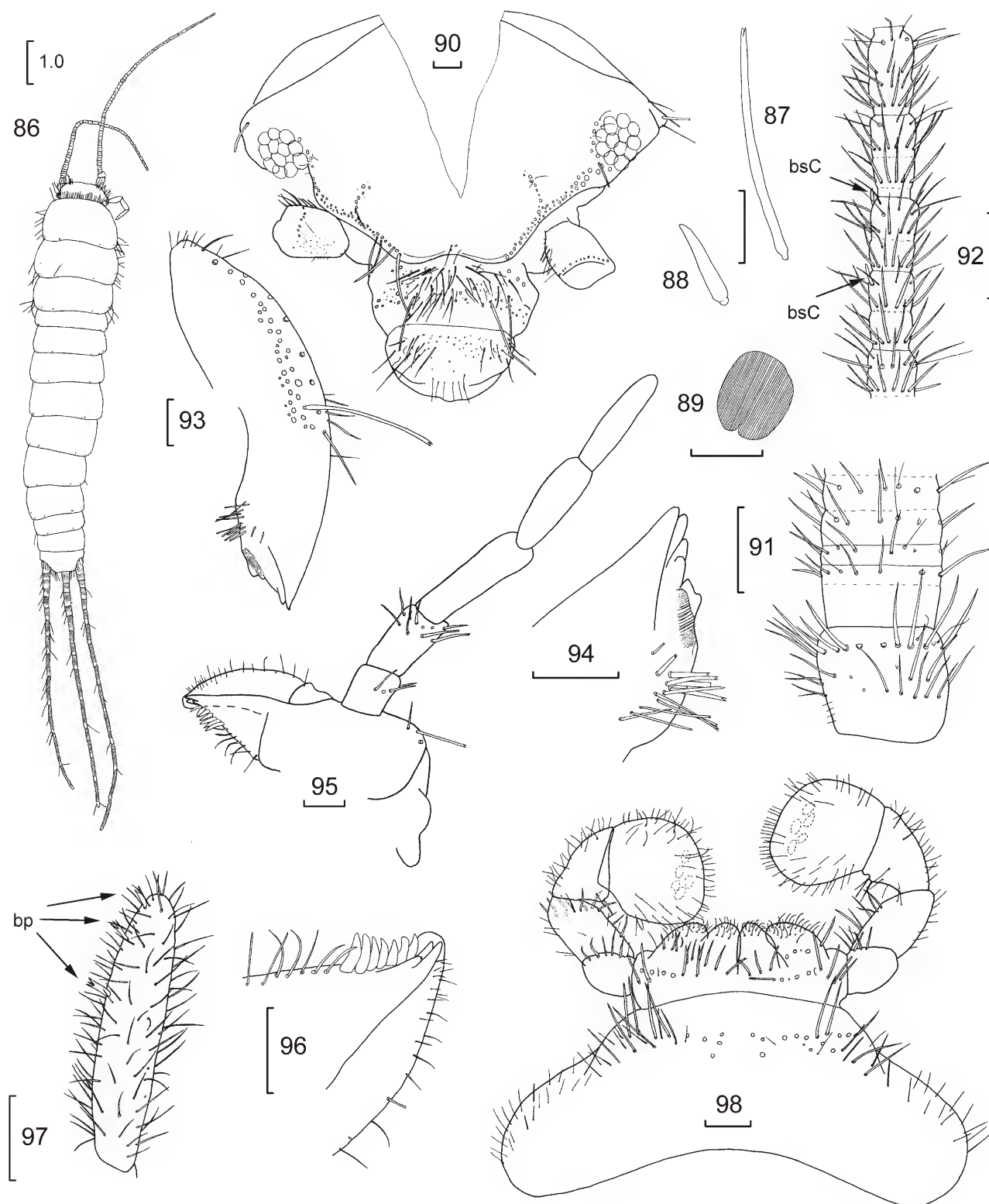
Scales: Quite broad, brown with numerous subparallel ribs that do not surpass the margin of the scale (Fig. 89). Scales found on top of head, some, either side of the tiny medial setae protruding well beyond the anterior margin; scales absent from clypeus and labrum as well as all cephalic appendages; dark scales present on all nota and abdominal tergites, clear scales on all thoracic and abdominal sterna, and coxae of legs, absent from styli. Lanceolate scales present on all femora and tibia; other leg articles without scales; lanceolate scales also present on basal third of the terminal filaments (except basal few divisions).

Head: Wider than long (Fig. 90), without distinct bushes. Anterior margin without macrochaetae except for four tiny setae in the middle; strong macrochaetae along lateral margins with peri-antennal groups of about seven macrochaetae which are contiguous laterally with the rows of macrochaetae along the margin, the marginal macrochaetae continue along the sides of the head behind the antennae with a line of four or five macrochaetae lying above the eyes. Clypeus with some longer macrochaetae and several setae extending across the face. Labrum with many setae across the proximal half and a line of six thinner setae anteriorly. — Scape quite short with a subdistal line of setae and smaller setae over the dorsal anterior face, pedicel (Fig. 91) short, also with a subapical rosette of small macrochaetae with setae scattered over the surface medially; first annulus of flagellum apparently glabrous, subsequent annuli with a rosette of small setae and some short trichobothria, the divisions between the annuli difficult to discern in the slide mounted material, the intervals split into two annuli by the 7th interval, into four by the 12th and into eight by the 17th. Most distal surviving intervals (Fig. 92) divided into repeated patterns of eight annuli, each with two rosettes of setae, those basally long tapering, those distally thinner and almost parallel-sided, the apical article of each interval has at least one trichobothrium, the second and fourth annuli bear at least one long, sausage-shaped basiconic sensillum

(Type C of Adel, 1984). — Mandibles (Figs 93, 94) typical for Heterolepismatinae with well-developed molar and incisor regions; a group of about six strong and short plus five thinner, apically bifurcated setae distally adjacent to the molar region and a bush of about 40 macrochaetae externally. — Maxilla (Fig. 95) with three apically bifurcate macrochaetae externally proximal to the palp; lacinia short and wide, with three strong teeth, one set further back than the other two, followed by about seven lamellate processes and a row of seven setae, galea with only short fine setulae (Fig. 96); apical article of maxillary palp (Fig. 97) 4.6 times longer than wide and 1.2 times longer than the penultimate article, the ultimate article with three branched papillae, other specialised sensilla (e.g., basiconic sensilla) not seen, last three articles of palp with fine setae only, two basal articles with subapical rosettes of thicker setae. — Labium (Fig. 98) wider than long, postmentum with setae scattered in band across entire width including several small setae along and near the anterolateral margins, prementum with transverse and oblique groups of strong setae and with short setulae distally; apical article of labial palp (Fig. 99), about as wide as long (L/W 0.95), with five papillae of the compact type arranged in a broad three plus two cluster arrangement, the distal three arranged in a curved line, a single basiconic sensillum (Type C) on the outer margin near the level of the papillae, covered with numerous fine short setae especially below; penultimate article with some stronger setae on the bulge medially; second article also with stronger setae along the inner margin and a subapical rosette; basal article with an apical line of stronger setae ventrally.

Thorax: Pronotum (Fig. 100) with complete setal collar of short macrochaetae and some cilia; setae of lateral margins lost, but consisting of some marginal setae as well as cilia and two submarginal macrochaetae, one about one quarter the distance along the margin and the other about seven-eighths along the margin associated with the posterior trichobothrial area. Anterior trichobothrium a little further than half way along the margin, with two to four setulae posterior to the trichobothrium, not associated with a macrochaeta (Fig. 101). The posterior trichobothrium mediad of a submarginal macrochaeta and its cilium, with two or three setulae posterior to this group (Fig. 102). Posterior margin with 1+1 single macrochaetae each associated with two cilia (Fig. 103). — Mesonotum (Fig. 104) also with small setae along the margins as well as three combs each of two macrochaetae anterior to the anterior trichobothrial area, both trichobothrial areas (Fig. 105) are more posterior than on the pronotum, the anterior trichobothrium located about $\frac{1}{2}$ the distance along the margin and not associated with any macrochaeta and the posterior area as in the pronotum; 1+1 posterior macrochaetae as in pronotum. — Metanotum (Figs 106, 107) similar to mesonotum.

Presternum with transverse row of strong macrochaetae (Fig. 108) as well as some simple cilia. All thoracic sterna with hyaline scales. — Prothoracic sternum (Fig. 108) cordiform, slightly wider than long (L/W 0.91), 1+1 irregular combs of eight to nine bifurcate macrochaetae running subparallel to the margin, as well as some marginal setae and cilia in distal one quarter, short posterior margin between combs straight. — Mesosternum (Figs 109) sub-parabolic, as long as wide at its base, (L/W 1.01) with about eight macrochaetae forming an irregular submarginal row along the posterior quarter of the margin, short posterior margin

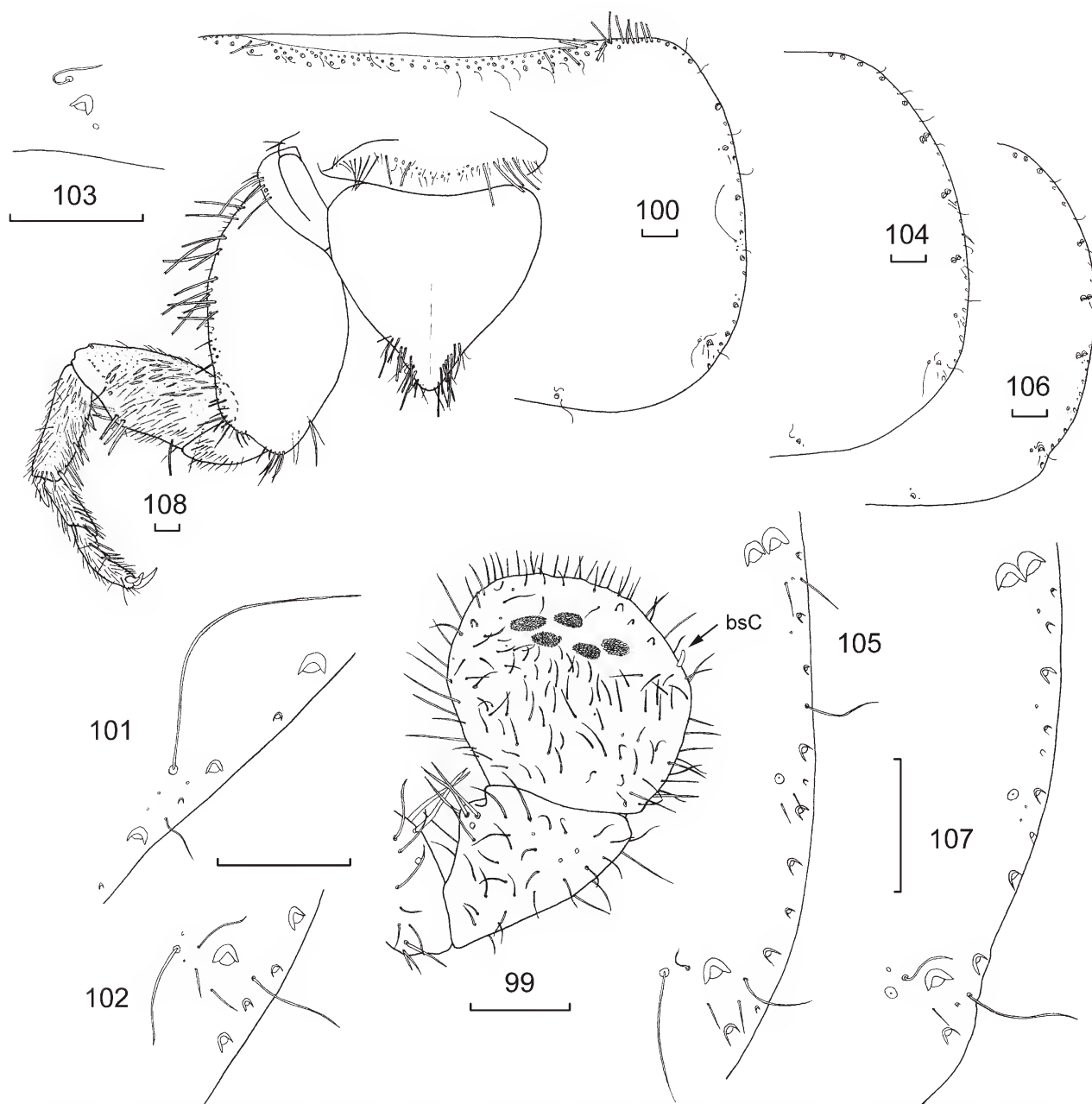


Figures 86–98. *Heterolepisma pyramidum* sp. nov. holotype specimen K.261254 ♀ (86) habitus; (87) smooth, apically bifurcate macrochaeta of PI coxa; (88) carrot-shaped macrochaeta of PI tibia; (89) scale from mesonotum; (90) head; (91) antenna, pedicel and basal intervals of flagellum; (92) idem, most distal surviving interval showing basiconic sensilla type C (bsC); (93) mandible; (94) idem, incisor and molar regions; (95) maxilla, only more prominent setae of palp illustrated; (96) idem, lacinia and galea; (97) idem, apex of ultimate article of palp with its three branched papillae (bp); (98) labium. Scale bars = 0.1 mm unless otherwise indicated.

between combs straight. — Metasternum (Fig. 110) wider than long (L/W 0.74), apically a little truncate, 1+1 apical combs of about five macrochaetae, the distance between the combs 2.3 times the average length of each comb (range

2.1–2.6), lateral margins with a few simple setae and cilia only adjacent to the combs.

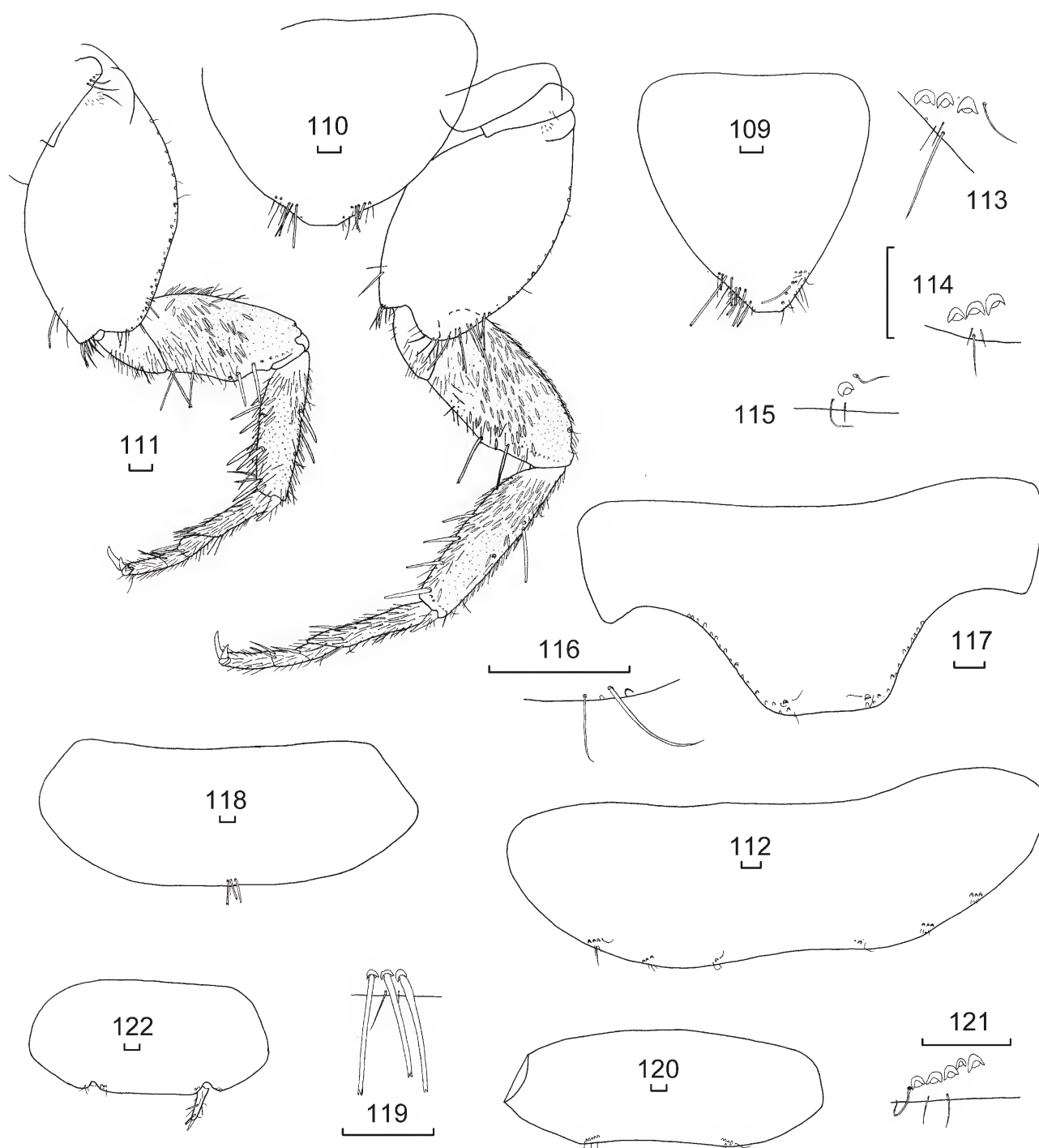
Legs (Figs 108, 110, 111) becoming progressively longer and more slender with the tibia of PII being 1.3 times longer



Figures 99–108. *Heterolepisma pyramidum* sp. nov. holotype specimen K.261254 ♀ (99) ultimate article of labial palp showing basiconic sensillum (bsC); (100) pronotum, anterior and right margins; (101) idem, right anterior trichobothrial area; (102) idem, right posterior trichobothrial area; (103) idem, left posterior comb; (104) mesonotum, right side; (105) idem, trichobothrial areas, right side; (106) metanotum, right side; (107) idem, trichobothrial areas, right side; (108) presternum, prothoracic sternum and PI. Scale bars = 0.1 mm.

than that of PI and the tibia of PIII being 1.8 times longer than that of PI, tibia L/W ratio of legs PI 2.9, PII 3.2, PIII 3.6; tarsi L/W ratio PI 5.3, PII 8.0, PIII 9.2. Precoxa of PI with lateral combs of four macrochaetae. — Coxa of PI (Fig. 108) without comb near the anterolateral corners, but many strong macrochaetae in approximately two rows along the external margin, becoming shorter distally; inner margin with five macrochaetae distally over the articulation and another seta subdistally near three long thin setae on the dorsal face. — Trochanter with small setae. — Femur ventrally with one large macrochaeta near the trochanter and three large bifurcate carrot-shaped macrochaetae plus two strong simple macrochaetae on the posterior bulge, distal anterior corner with two macrochaetae, lanceolate scales along the margin and extending onto the ventral face of the femur in the anterior

half, rest of ventral surface with fine scattered setae. — Tibia with a few lanceolate scales on the ventral face proximally, rest of surface with setae, a strong carrot-shaped macrochaeta distally as well as a thinner pair subdistally, another pair midway along the margin and a smaller pair near the proximal end of the posterior margin, distal end of tibia with a row of stronger setae, anterior margin with two stout macrochaetae about one third and two thirds along the margin, as well as smaller setae; apical spine with several setae, some quite strong. — Tarsi of four articles, the basal tarsal article of PI not quite as long as the remaining articles together, bearing some stronger setae below and many other smaller setae over the surface; second and third articles the shortest, each with two stronger setae ventrally. Pretarsus with two long curved lateral claws and a shorter straight medial claw. PII (Fig.

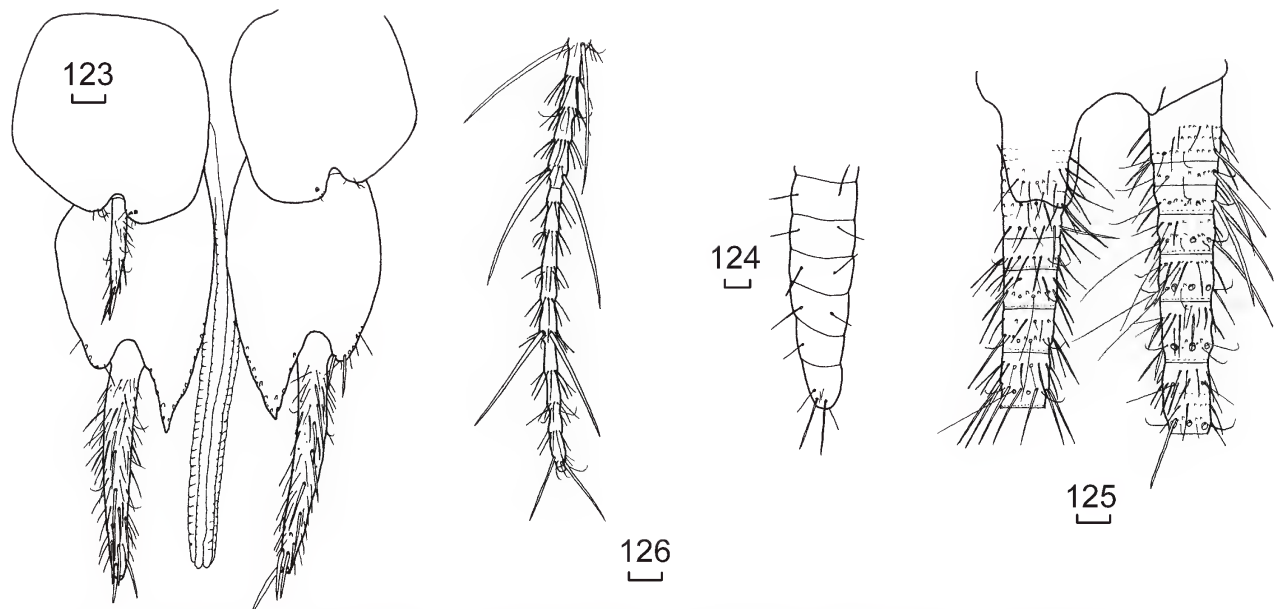


Figures 109–122. *Heterolepisma pyramidum* sp. nov. holotype specimen K.261254 or K.261255 ♀ (109) mesothoracic sternum; (110) metathoracic sternum and PIII; (111) PII; (112) urotergite III; (113) urotergite VII, left lateral comb; (114) idem, left sublateral lateral comb; (115) idem, left submedial comb; (116) urotergite IX, left infralateral comb; (117) urotergite X; (118) urosternite I; (119) idem, medial comb; (120) urosternite IV; (121) right comb of urosternite IV; (122) urosternite VII. Scale bars = 0.1 mm.

111) similar to PI except coxae with fewer macrochaetae along the outer margin, only becoming two macrochaetae wide in the distal half, with about seven stout setae over the articulation, the tibia with three stout macrochaetae along the dorsal margin and the first tarsal article is longer than the remaining three together, and PIII (Fig. 110) similar to PII but areas of lanceolate scales more extensive.

Abdomen: Urotergite I with 2+2 combs, the lateral combs of two macrochaetae each associated with three marginal

setae and a setula, the submedial combs with one or two marginal setae, 0–3 setulae and a cilium on the laterad end of each comb; urotergites II–VII (Fig. 112) with 3+3 small combs as shown in table 7, each lateral comb associated with 1–3 marginal setae, 1–3 setulae, usually a cilium at the mediad end of each comb and sometimes one between, and anterior to, the two most mediad macrochaetae, each sublateral comb with 0–2 marginal setae and 1–3 setulae, the submedial combs usually with a cilium on either side of the single macrochaeta and rarely a setula between the



Figures 123–126. *Heterolepisma pyramidum* sp. nov. holotype specimen K.261254 ♀ (123) coxites VIII and IX, with styli and ovipositor; (124) apex of ovipositor valve; (125) base of cercus and medial dorsal appendage; (126) apex of cercus. Scale bars = 0.1 mm.

macrochaeta and the margin (Figs 113–115); urotergite VIII with 2+2 combs, lacking the sublateral comb; urotergite IX without combs but with two delicate marginal setae and two cilia in each infralateral corner (Fig. 116). Urotergite X (Fig. 117) short and distinctly trapezoidal (L/W about 0.35), with 1+1 macrochaetae in the posterolateral corners, each associated with cilia on each side and numerous setae along the margins.

Urosternite I with a medial comb of three macrochaetae and two setulae on a non-protruding region (Figs 118, 119), urosternite II–VI (Figs 120, 121) with 1+1 lateral combs each of four or five macrochaetae and two marginal setulae plus a cilium at the laterad end of each comb, the distance between each comb is about nine times the average length of the combs on the segment (range 8.7–10.2), urosternite VII (Fig. 122) with styli, 1+1 combs each of two macrochaetae located mediad of each stylus, associated with two marginal setulae, laterad of the stylus is a cilium associated with two marginal setulae. Urosternite VIII in ♀ divided into separate coxites shaped as shown in figure 123, each bearing a small stylus which is apically armed with some strong setae, one or two macrochaetae mediad of the stylus insertion associated with a few small marginal setae, with two or three setae and a cilium on the outer side of the stylus. Styli present in three pairs, those on IX about twice as long as those on VIII which

are just a little longer than those on VII.

Coxite IX of ♀ (Fig. 123) with the internal process acute apically, about three times longer than the external process and 1.3 times as long as wide at its base, reaching to about one third the length of the stylus; external and internal margins of internal process and external margin with a few moderately strong setae, apex of outer process with three or four strong setae. — Ovipositor (Fig. 123) probably not yet fully developed as its only reaches the end of the styli (1.20 HW), composed of about 45 divisions (range 44–47). Distal divisions of gonapophyses difficult to see adequately in prepared material (Fig. 124) with only short fine setae and setulae.

Cerci (Figs 125, 126) with basal divisions as long as wide (or perhaps it is several divisions with indistinguishable sutures), divisions two to four shorter than wide, fifth division as long as wide consisting of two annuli and first lanceolate scales seen, following division s consisting of four annuli eventually increasing to eight annuli with the setae, macrochaetae and trichobothria becoming increasingly stronger and longer, lanceolate scales not visible in distal two thirds of cerci and not seen on median dorsal appendage. — Median dorsal appendage (Fig. 128) similar.

Male: Unknown.

Table 7. Number of macrochaetae per bristle comb—*Heterolepisma pyramidum* sp. nov.

segment	urotergite			urosternite	
	lateral	sublateral	submedial	medial	lateral
I	2	1–2	—	3	—
II	3	3	1	—	4
III	3	3	1	—	4–5
IV	3–4	3	1	—	4–5
V	4	3	1	—	4–5
VI	4	3	1	—	5
VII	3–4	3	1	—	2
VIII	3	—	1	—	1–2

Habitat. Collected on a remote rock pyramid, the remnant of an old volcanic cone.

Etymology. Named after the dramatic appearance of the island from which this species was collected.

Remarks

Even though only a single subadult female specimen was available, the species is described as new because it has a clear morphological difference to the published description of its probable nearest neighbour (*H. rouxi* from New Caledonia) and good molecular sequence data are available for it. *Heterolepisma rouxi* is in need of redescription as characters such as the chaetotaxy of the anterior margin of the frons, the position of the trichobothrial areas of the nota and the presence or absence of lanceolate scales were not reported. *Heterolepisma heraldense* sp. nov., described below, while distinct from *H. pyramidum* sp. nov., may eventually be shown to be conspecific with *H. rouxi* when the latter species is redescribed according to current criteria.

The character analysis places *H. pyramidum* sp. nov. in a clade with *H. parvum*, *H. heraldense* sp. nov. and *H. serranoi* which all have a glabrous anterior margin to the frons, lanceolate scales, a medial comb on urosternite I and sublateral combs on urosternites II–VII consisting of more than one macrochaeta. The limited molecular data available for *H. parvum* (28S of three specimens) and one specimen of *H. pyramidum* sp. nov. offers no support for this arrangement (see supplementary data on Figshare).

Heterolepisma heraldense sp. nov.

<http://zoobank.org/NomenclaturalActs/BA3F1745-78BD-407A-9689-147387B73842>

Figs 127–168

Holotype. ♀ (HW 1.00) (AM K.261309 on one slide) CORAL SEA TERRITORY: South West Herald Cay, 16.98°S 149.13°E, 17.v.2007, R. Farrow. **Paratypes.** juvenile ♂ (HW 0.80) (K.261310 on one slide) same data as holotype; juvenile ♀ (HW 0.70) (K.377828 in alcohol) CORAL SEA TERRITORY: North East Herald Cay, 16.943°S 149.199°E, 16.v.2007, P. Greenslade & R. Farrow.

Diagnosis. As for *H. pyramidum* sp. nov., described above, from which it can easily be distinguished by its smaller size (6 mm for an apparently mature female vs almost 9 mm for an apparently subadult female), the posterior combs of the nota (but not the urotergites) which each consist of a larger macrochaeta and a sizable, but smaller, submarginal insertion (compared to just a single macrochaeta), the location of the anterior trichobothrial areas of the meso- and metanota about $\frac{3}{4}$ the distance along the margins (versus $\frac{1}{2}$), the smaller number of combs of two macrochaetae on the lateral margins of the meso- and metanota (three and two versus two and one respectively), the shorter wider legs (e.g., femur PII L/W 1.8 versus 2.4 and tarsi PIII L/W 6.1 versus 9.2), the presence of 3+3 combs on urotergite I (versus 2+2) and the smaller number of divisions in the ovipositor (circa 37 versus circa 45).

This species may however eventually prove to be a synonym of *H. rouxi* Silvestri, 1915 for which the original description is inadequate.

Description

Appearance: Small to medium sized silverfish, thorax about 7% wider than abdomen which only tapers slightly posteriorly from about the fifth abdominal segment (Fig. 127); appearance when live unknown.

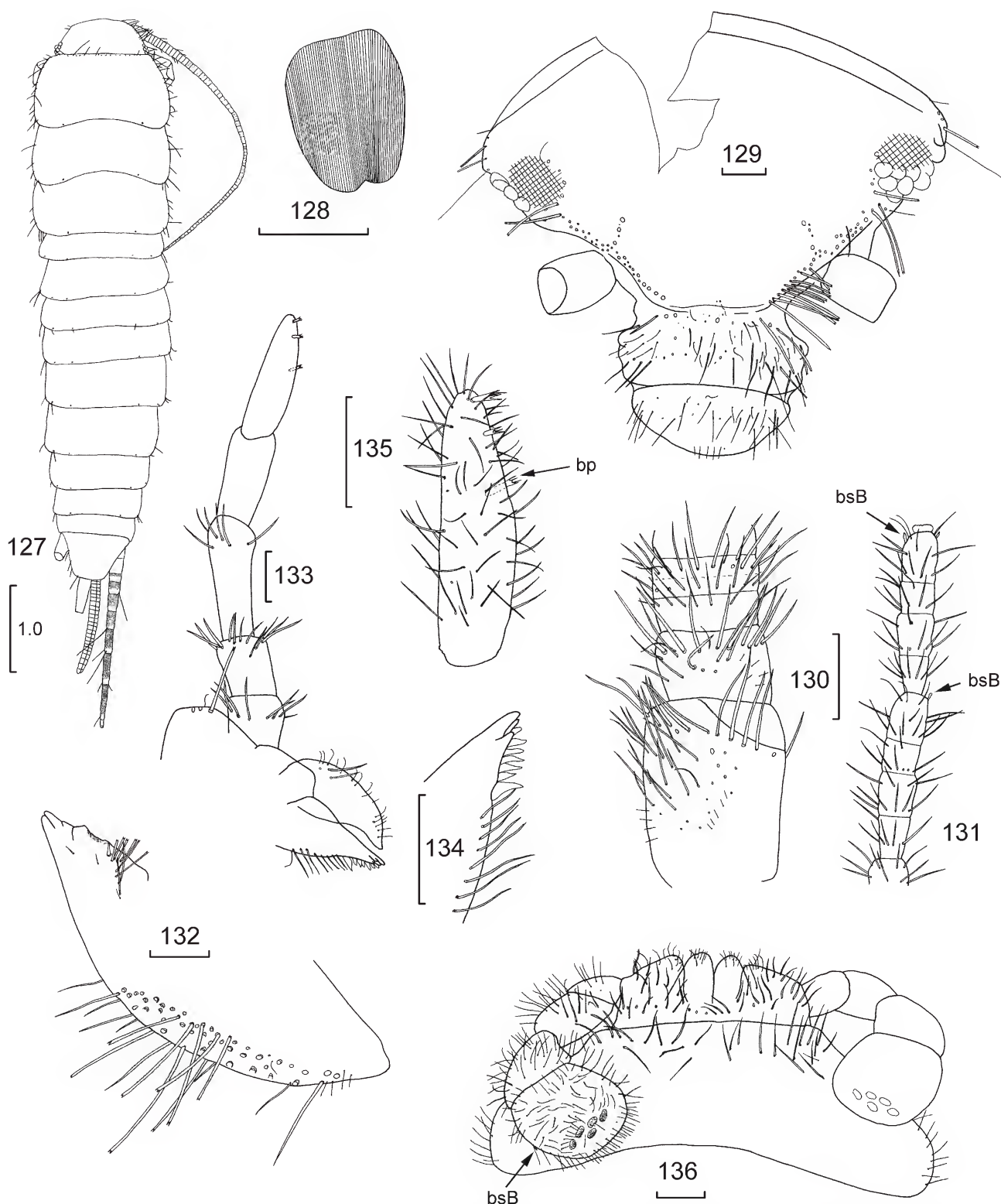
Body length: H+B 5.9 mm; HW 1.00 mm; thorax: length 1.9 mm or 0.32 H+B; width up to 1.45 mm, meso- and nota of same width with the pronotum just slightly narrower, pronotum longer than meso- and metanota; antennae incomplete at 4.1 mm or > 0.7 H+B; cerci and median dorsal appendage largely damaged at 1.9 mm and 0.7 mm (>0.32 and >0.12 H+B) respectively.

Pigmentation: Pigment brownish. Flagellum of antennae evenly pale becoming slightly darker distally; pedicel and scape without pigment. Terminal filaments annulated darker brown with only the most distal portion of each major division from just below the rosette of major macrochaetae to the suture with the next division devoid of pigment. Head with very small area of pigment around eyes only. Clypeus, labrum and mandibles without pigment. Maxillary palp without pigment except for slightly darker penultimate article. Labium and labial palp largely without pigment except for small amount along the outer margin of the penultimate article. Legs without pigment except for dorsal face of the tibia and the first tarsal article where light pigment is fairly evenly distributed. Urotergite X with light pigment, darkest proximally and becoming lighter distally. Sternites including coxites IX and styli without obvious pigment. Ovipositor without pigment.

Macrochaetae: Smooth, hyaline or slightly straw coloured, apically bifurcate with truncated tips to each bifurcation. Some macrochaetae on tibia, stout carrot-shaped.

Scales: Quite broad, brown with numerous subparallel ribs that do not surpass the margin of the scale (Fig. 128). Scales found on top of head; scales absent from clypeus and labrum as well as all cephalic appendages; dark scales present on all nota and abdominal tergites, clear scales on all thoracic and abdominal sterna, and coxae of legs, absent from styli. Lanceolate scales present on all femora and tibia; other leg articles without scales; lanceolate scales not unambiguously observed on basal third of the terminal filaments.

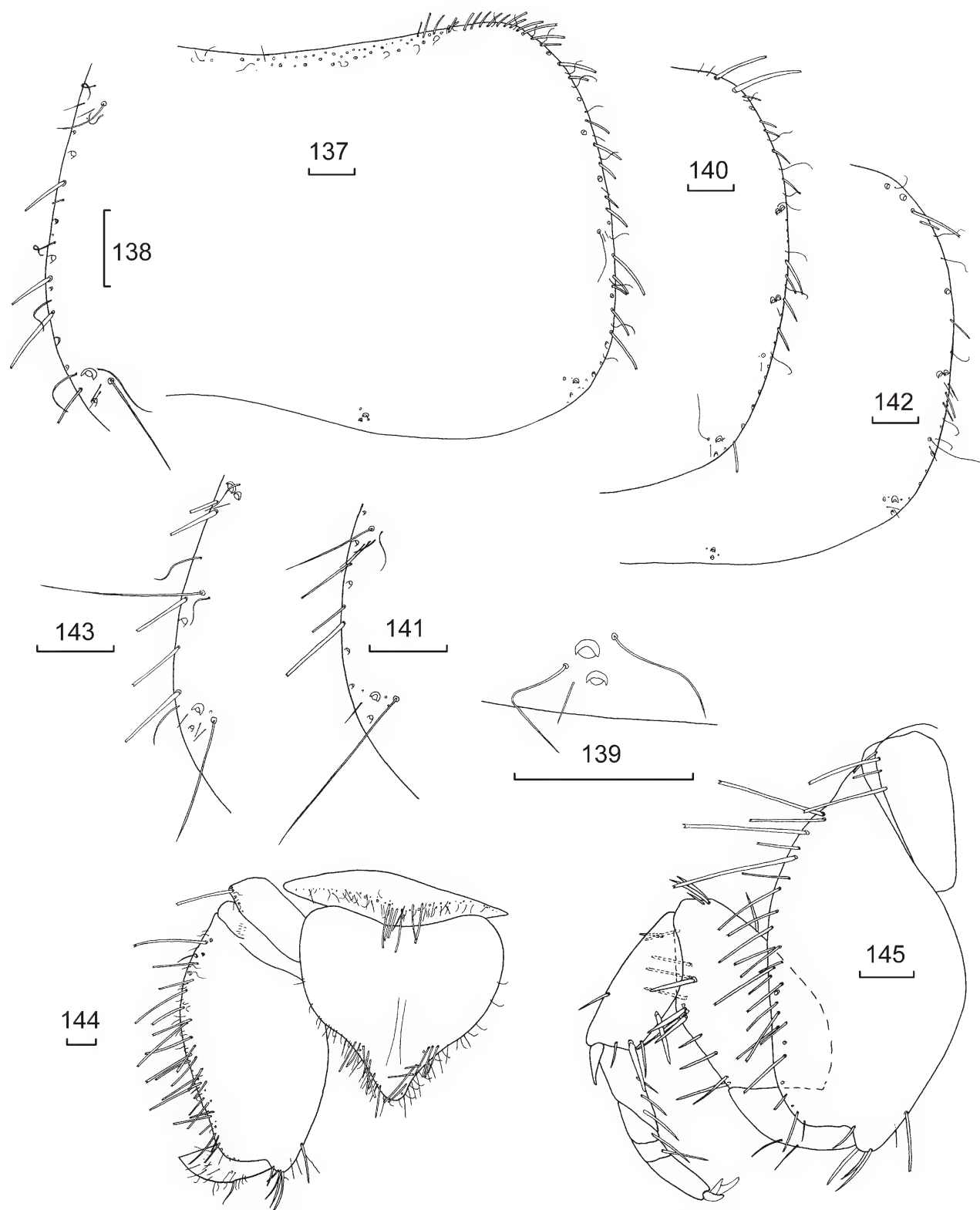
Head: Wider than long (Fig. 129), without distinct bushes. Anterior margin without macrochaetae except for two or three tiny setae in the middle; strong macrochaetae along lateral margins with peri-antennal groups of two or three larger macrochaetae as well as some cilia, only weakly connected with the one to two rows of macrochaetae along the margin, the marginal macrochaetae continue along the sides of the head behind the antennae with a line of four or five macrochaetae lying above the eyes. Clypeus with some longer macrochaetae in 1+1 rows of about three macrochaetae laterally and close to the frons as well as numerous setae across the face; lanceolate scales not observed. Labrum with many setae across the middle of the face a line of six thinner setae anteriorly. — Scape (Fig. 130) quite short with a subdistal line of setae and smaller setae over the dorsal anterior face, pedicel short, also with a subapical rosette of small macrochaetae with a few setae scattered over the surface medially; first annulus of flagellum with a subapical rosette of fine setae, subsequent annuli with a single rosette of setae, the divisions between



Figures 127–136. *Heterolepisma heraldense* sp. nov. holotype specimen K.261309 ♀ (127) habitus; (128) scale from urotergite VII; (129) head (cross-hatched area obscured by eye pigment); (130) antenna, scape, pedicel and basal intervals of flagellum; (131) idem, most distal surviving interval showing basiconic sensilla (**bsB**); (132) mandible (poorly orientated); (133) maxilla, only more prominent setae of palp illustrated; (134) idem, lacinia; (135) idem, ultimate article of palp with its three branched papillae (**bp**); (136) labium. Scale bars = 0.1 mm unless otherwise indicated.

the annuli difficult to discern in the slide mounted material, the intervals split into two annuli by the 7–9th interval. Most distal surviving intervals (Fig. 131) divided into repeated patterns of four or possibly eight annuli, the basal interval with a single rosette of small fine setae, the second and third

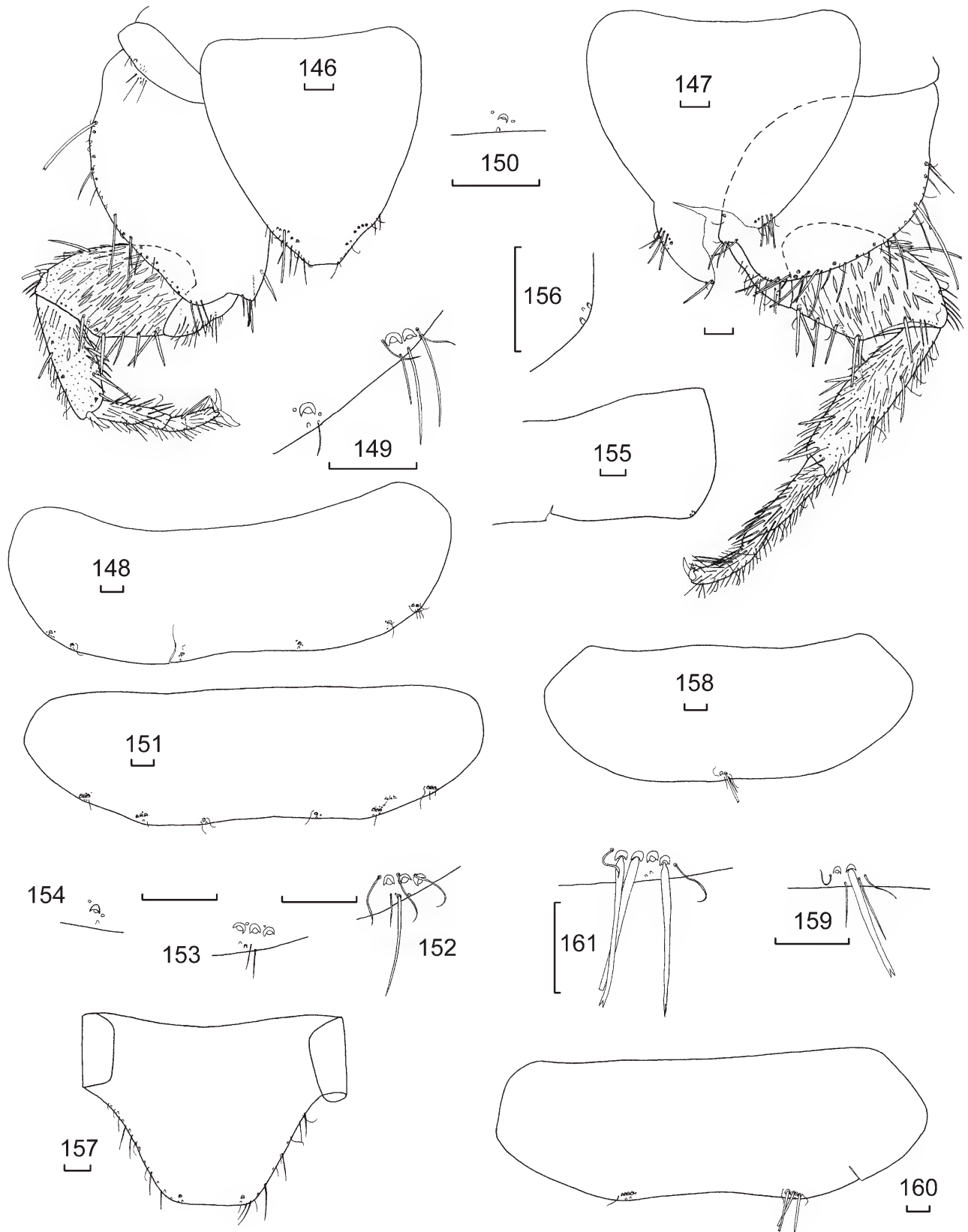
with two similar rosettes, the ultimate article of each interval with two rosettes of small setae and a further subapical rosette of fine, curved-tipped setae and one or two basiconic sensilla (type B). Trichobothria were rarely observed in the most apical rosettes of each interval making it difficult to determine the



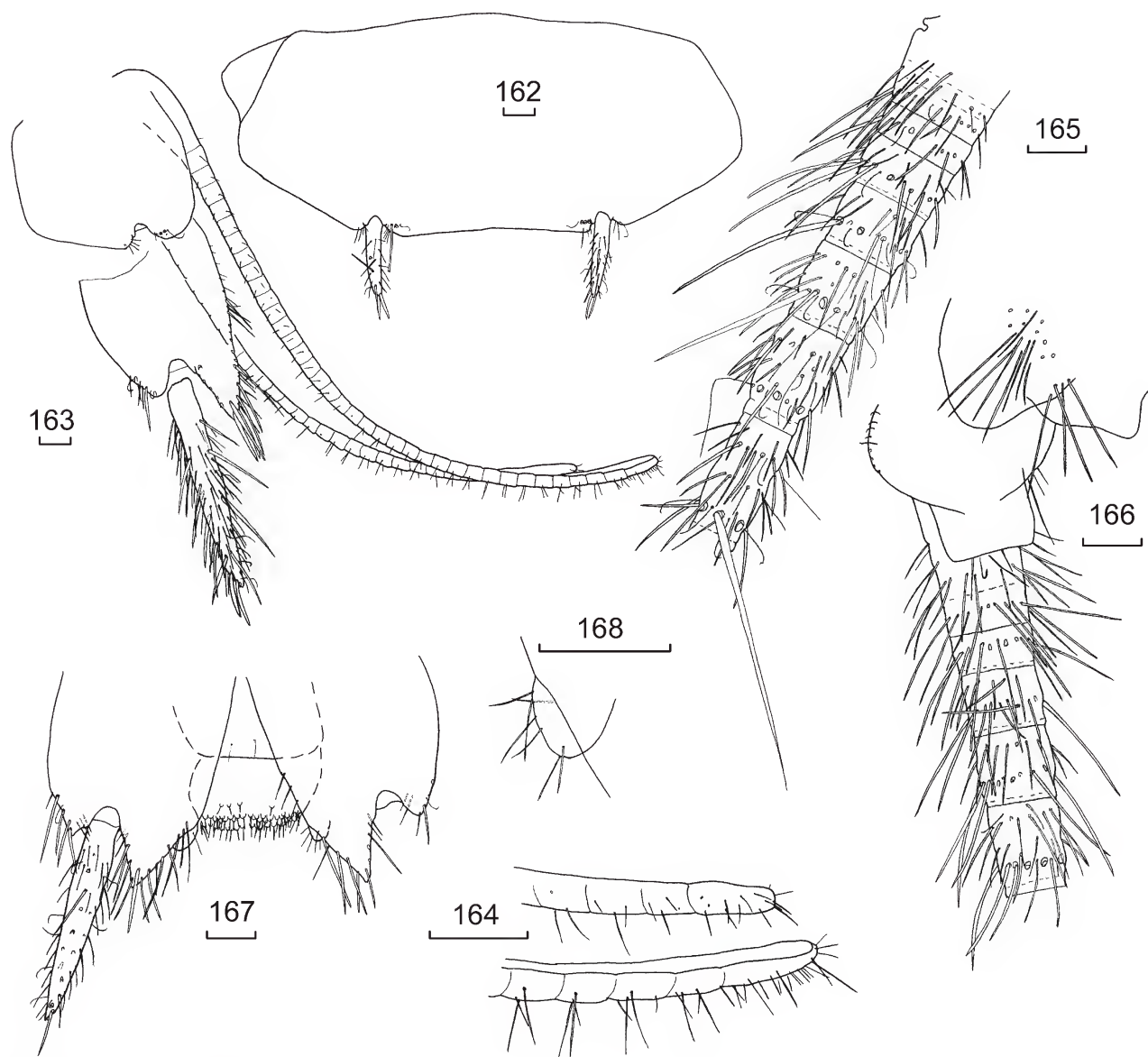
Figures 137–145. *Heterolepisma heraldense* sp. nov. holotype ♀ specimen K.261309 unless otherwise noted by specimen number (137) pronotum; (138) idem, trichobothrial areas of left side; (139) idem, left posterior comb; (140) mesonotum, right side; (141) idem, trichobothrial areas, left side; (142) metanotum, right side; (143) idem, trichobothrial areas, left side; (144) presternum, prothoracic sternum and coxa of PI; (145) PI of K.261310. Scale bars = 0.1 mm.

number of annuli per interval. — Mandibles (Fig. 132) aligned on slide so that the molar areas of both mandibles are difficult to discern but appear to be typical for *Heterolepismatinae* with well-developed molar and incisor areas; a group of about seven strong and short plus four thinner, apically bifurcated

setae distally adjacent to the molar region and a bush of about 60 macrochaetae externally. — Maxilla (Figs 133, 134) with three apically bifurcate macrochaetae externally proximal to the palp; lacinia short with three strong teeth, one set further back than the other two, followed by about seven lamellate



Figures 146–161. *Heterolepisma heraldense* sp. nov. holotype ♀ specimen K.261309 (146) PII and mesothoracic sternum; (147) PIII and metathoracic sternum; (148) urotergite I; (149) idem, right lateral and sublateral combs; (150) idem, right posterior comb; (151) urotergite VII; (152) right lateral comb of urotergite IV; (153) right sublateral comb of urotergite IV; (154) right submedial comb of urotergite IV; (155) urotergite IX, right side; (156) idem, detail of infralateral comb; (157) urotergite X; (158) urosternite I; (159) idem, medial comb; (160) urosternite III; (161) idem, left comb. Scale bars = 0.1 mm.



Figures 162–168. *Heterolepisma heraldense* sp. nov. holotype ♀ specimen K.261309 unless otherwise noted by specimen number (162) urostermite VII with styli; (163) right coxites VIII and IX, with stylus IX and ovipositor; (164) apex of ovipositor valves; (165) base of cerci; (166) base of medial dorsal appendage; (167) coxites IX of ♂ K.261310; (168) left paramere. Scale bars = 0.1 mm.

processes and a row of eight setae, galea with short fine setulae as well as two or three setae basally; apical article of maxillary palp (Fig. 135) only 2.9 times longer than wide (range 2.1–4.0) and 1.3 times longer than the penultimate article (range 1.1–1.5), the ultimate article with three branched papillae, other specialised sensilla (e.g., basiconic sensilla) not seen, last two articles of palp with fine setae only, two basal articles with subapical rosettes of thicker setae, third article also with rosette but setae not as thick as those on two basal articles. — Labium (Fig. 136) much wider than long, postmentum with fine setae along the lateral margins and longer slightly strong thin simple setae scattered in band across entire width anteriorly, prementum with transverse and oblique groups of strong simple setae and with short setulae distally; apical article of labial palp, about as wide as long (range L/W 0.95–1.12), covered with numerous fine short setae, with five papillae of the compact type arranged in a three plus two cluster arrangement, the distal three arranged in a curved line, a small single basiconic sensillum (type C)

on the outer margin proximal to the level of the papillae; penultimate article with some longer but not much stronger setae on the bulge medially; second article also with similar setae; basal article with smaller setae only.

Thorax: Pronotum (Fig. 137) with complete setal collar of short macrochaetae and some cilia; lateral margins with marginal setae as well as cilia and two submarginal macrochaetae, one about $\frac{1}{4}$ the distance along the margin and the other about $\frac{3}{4}$ along the margin associated with the posterior trichobothrial area. Anterior trichobothrium a little further than half way along the margin with two or three setulae laterad and posterior to the trichobothrium, not associated with a macrochaeta (Fig. 138). The posterior trichobothrium mediad of a submarginal macrochaeta and its cilium, with two or three setulae posterior to this group (Fig. 138). Posterior margin with 1+1 combs composed of one larger macrochaeta insertion associated with two cilia and a smaller seta insertion posterior and mediad of the larger macrochaeta (Fig. 139). — Mesonotum (Fig. 140) also with

small setae along the margins as well as two combs each of two macrochaetae anterior to the anterior trichobothrial area; the more medial macrochaeta only half the length of the outer macrochaeta. Both trichobothrial areas are more posterior than on the pronotum (Fig. 141), the anterior trichobothrium located about $\frac{3}{4}$ the distance along the margin not associated with any macrochaeta and the posterior area as in the pronotum; 1+1 posterior macrochaetae as in pronotum. — Metanotum (Figs 142, 143) similar to mesonotum but with only a single comb of two macrochaetae.

Presternum with transverse row of setae and cilia across the entire width, the middle region with strong macrochaetae (Fig. 144). All thoracic sterna with hyaline round scales. — Prothoracic sternum (Fig. 144) cordiform with distinct concave margins in distal half as well as being longitudinally slightly concave, slightly wider than long (L/W 0.86), 1+1 irregular combs of six bifurcate macrochaetae running subparallel to the margin, as well as some marginal setae and cilia in distal three quarters. — Mesosternum (Figs 146) sub-parabolic as long as wide at its base, (L/W 1.03) with about six macrochaetae forming an irregular submarginal row along the posterior quarter of the margin, short straight posterior margin between combs. — Metasternum (Fig. 147) wider than long (L/W 0.80), apically round, 1+1 apical combs of five or six macrochaetae, the distance between the combs two to three times the average length of each comb (range 2.2–3.0), lateral margins with a few simple setae and cilia only adjacent to the combs.

Legs (Figs 144–147), PI lost beyond trochanter in holotype but legs becoming progressively long tibia PI/PIII of juvenile paratypes 0.64, tarsi PI/PIII 0.76; tibia L/W ratio of legs PI 2.4 (range 2.3–2.6), PII 2.6 (range 2.3–2.8), PIII 3.3 (range 2.8–3.6); tarsi L/W ratio PI 5.3 (range 4.8–5.8), PII 5.1 (range 4.9–5.4), PIII 6.1 (range 5.6–6.3). Precoxa of PI with lateral combs of four macrochaetae. — Coxa of PI (Figs 144, 145) with ill-defined comb of two macrochaetae near the anterolateral corners, many strong macrochaetae in approximately two rows along the external margin, becoming shorter distally; inner margin with about five short macrochaetae distally over the articulation and another robust seta subdistally near three long thin seta on the dorsal face. — Trochanter with two or three stronger setae as well as small setae and setulae. — Femur quite broad (L/W 1.8–2.0) ventrally with two large macrochaetae near the trochanter and four large macrochaetae on the posterior bulge with two equally spaced macrochaetae between these groups, subdistal anterior corner with two macrochaetae; three or four longer, strong setae along the posterior margin distal of the posterior bulge; lanceolate scales along the margin and extending

onto the ventral face of the femur in the anterior half, rest of ventral surface with fine scattered setae. — Tibia may have a few lanceolate scales on the ventral face proximally but the quality of the material available makes it difficult to be certain, rest of surface with setae, a strong carrot-shaped macrochaeta distally, another pair just beyond midway along the margin, the presence of a smaller pair near the proximal end of the posterior margin cannot be determined, anterior margin probably with one or two stout macrochaetae about one third along the margin and another pair two thirds along the margin, as well as smaller setae; apical spine with several setae. — Tarsi of four articles, the basal tarsal article of PI not quite as long as the remaining articles together, bearing some long, stronger setae below and many other smaller setae over the surface; second and third articles the shortest, each with two long, stronger setae ventrally. Pretarsus with two long curved lateral claws and a shorter straight medial claw. — PII (Fig. 146), coxa similar to PI except with fewer macrochaetae along the outer margin, only becoming two macrochaetae wide in the distal half, with about five stout setae over the articulation, trochanter with simple, but long setae. Femur short and wide (L/W 1.8) with about ten stout macrochaetae along the posterior margin as illustrated, lanceolate scales along the margin and extending onto the ventral face of the femur in the anterior half, rest of ventral surface with fine scattered setae. Tibia with a few lanceolate scales on the ventral face proximally, rest of surface with setae, with three stout macrochaetae along the dorsal margin and about five along the ventral margin. Tarsi quite short with long setae on the ventral surface, pretarsi with two long curved lateral claws and a shorter straight medial claw. — PIII (Fig. 147) similar to PII, femur short and wide (L/W 1.6–1.7), the first tarsal article being almost two thirds the total length of the tarsus. Tibia with long thin trichobothrium-like seta arising from the dorsal margin just forward of the most proximal dorsal macrochaeta (only seen in paratype K.261310), the hair being almost twice the width of the tibia in length.

Abdomen: Urotergites I–VII (Figs 148, 151) with 3+3 combs as shown in Table 8, although the submedial comb is absent on one side of urotergite I in the male paratype (K.261310), the lateral combs (Figs 149, 152) consisting of 1–3 macrochaetae each associated with 2–3 cilia, 1–2 marginal setae and 1–2 setulae, the sublateral combs (Figs 149, 153) of 1–3 macrochaetae each associated with 0–2 cilia, 1–2 marginal setae and 1–2 setulae, the submedial combs (Figs 150, 154) with two cilia and a marginal seta; urotergite VIII with 2+2 combs, lacking the sublateral comb; urotergite IX (Figs 155, 156) without combs but with three small marginal setae in each infralateral corner. Urotergite

Table 8. Number of macrochaetae per bristle comb—*Heterolepisma heraldense* sp. nov.

segment	urotergite			urosternite	
	lateral	sublateral	submedial	medial	lateral
I	1–2	1	0–1	2	—
II	2	2	1	—	2–3
III	2–3	2–3	1	—	3–4
IV	2–3	2–3	1	—	3–4
V	3	2–3	1	—	3–4
VI	3	3	1	—	3–4
VII	2–3	2–3	1	—	2–3
VIII	2	—	1	—	2–3

X (Fig. 157) short and distinctly trapezoidal (L/W about 0.46), with 1+1 macrochaetae in the posterolateral corners and several setae along the margins.

Urosternite I with a medial comb of two macrochaetae associated with a cilium at each end and a marginal seta and setula on a non-protruding region (Figs 158, 159); urosternites II–VI (Figs 160, 161) with 1+1 lateral combs each of two to four macrochaetae and with a cilium at each end of the comb, one or two marginal setae and 1–2 setulae, the distance between each comb is about twelve times the average length of the combs on the segment (range 10–14), urosternite VII (Fig 162) in ♀ with styli, 1+1 combs each of two or three macrochaetae located mediad of each stylus associated with a marginal seta and 2–3 marginal setulae, laterad of the stylus is a cilium associated with two marginal setulae. Urosternite VIII in ♀ divided into separate coxites shaped as shown in figure 163, each bearing a small stylus, 2–3 macrochaetae mediad of the stylus insertion associated with a few small marginal setae, with two or three setae and a cilium on the outer side of the stylus. Styli present in three pairs, those on IX about 1.5 times the length of those on VII.

Coxite IX of ♀ (Fig. 163) with apically acute internal process, about four times longer than the external process in the adult and 1.5 times as long as wide at its base, reaching to about one quarter length of the stylus; external and internal margins of internal with a few moderately strong setae, apex of round outer process with three or four strong setae. — Ovipositor appears fully developed surpassing the end of the stylus by about the length of the stylus (1.9 HW), composed of about 37 divisions. Distal divisions of gonapophyses (Fig. 164) with only short fine setae and setulae.

Cerci (Fig. 165) with basal divisions wider than long, divisions two to four with a single rosette of setae cilia and some trichobothria, fifth and sixth divisions each with two rosettes, the basal rosette of finer setae and trichobothria, following divisions consisting of three then four rosettes; most distal surviving divisions (probably only one third the length of the cercus) composed of four annuli each with two rosettes of setae, with large macrochaetae restricted to the most distal rosette. — Median dorsal appendage (Fig. 166) not well preserved; only about seven divisions remaining, most setae quite long and thin, macrochaetae restricted to the most distal rosette of each division. Lanceolate scales not observed on the terminal filaments.

Male: Based on specimen K.261310 which may be subadult: As for female but styli present only on segments VIII and IX, coxites IX (Fig. 167) with acute inner process about as long as wide at its base (range 0.95–1.04) and 1.8–2.7 times longer than the external process, reaching to just under half the length of the stylus; both processes also with several strong setae mostly apically emerging from both the dorsal and ventral surfaces of the processes close to or on the margin. Parameres a little shorter than wide, with only about ten short fine setae (Figs 167, 168). Penis typical for genus with numerous glandular setae apically, each set on a protuberance.

Habitat. The specimens were collected from both low coral cays that form the Herald Group. The specimen from NE Cay (K.377828) was extracted from *Abutilon* [fam. Malvaceae] leaf litter using a Tullgren funnel. The specimens from the SW Cay were labelled “HC S bark”.

Etymology. The species named *heraldense* referring to the type locality.

Remarks

Silvestri's 1915 description of the New Caledonian species *H. rouxi*, while diagnostically useful at the time it was written, is today inadequate. It lacks not only higher level details such as the chaetotaxy of the anterior margin of the frons and the presence or absence of lanceolate scales but also many smaller details such as the number of divisions in the ovipositor and the chaetotaxy of the lateral margins of the nota which could well reveal differences. *Heterolepisma heraldense* sp. nov. may eventually prove to be conspecific with *H. rouxi* although the illustrated urotergite X in the latter appears more rounded in the male. New Caledonia is some 1600 km south east of the Herald Cays.

Maritisma gen. nov.

<http://zoobank.org/NomenclaturalActs/56115144-6890-4115-88A2-9716C9C5EF95>

Type species. *Maritisma coralinium* sp. nov.

Diagnosis. Medium-sized silverfish. Body shape as in Fig. 169. Pigment apparently absent or very limited e.g., around eyes. Macrochaetae smooth with apical bifurcations. Scales multi-radiate, rounded with ribs not very close together; lanceolate or triangular scales apparently absent. Antennae possibly with rod-like basiconic sensilla. Chaetotaxy of frons consisting of a row of macrochaetae along anterior margin joining laterally with rows along the sides of the head which run back along the margin and up over the eyes, peri-antennal groups weak. Clypeus with longer macrochaetae laterally and across the face proximally, with small setae medially. Labrum with many macrochaetae distributed across the proximal half and some smaller setae in the anterior half. Eyes of about 12 ommatidia. Apical article of labial palp broad with 3+2 papillae of the aufgelöst type (individual subunits of each papilla not packed closely together), those more distal very long.

Pronotum with narrow setal collar which is largely interrupted medially. Thoracic nota with marginal setae and a few submarginal combs each of just a single or two macrochaetae; each lateral margin with two open trichobothrial areas, each anterior trichobothrial area of the pronotum with a macrochaeta laterad of the trichobothrium; posterior margin with 1+1 combs each of a single macrochaeta.

Thoracic sternites free, sub-parabolic with submarginal macrochaetae along the more distal lateral regions. Legs typical for the Heterolepismatinae; tarsi with four articles, pretarsi with two claws and a medial empodial claw. Urotergites I–VII with 3+3 small combs, urotergite VIII with 2+2 combs, urotergite IX with 1+1 sublateral setulae. Urotergite X very short, rounded with a few macrochaetae along each lateral margin. Urosternite I with medial comb, urosternites II–VIII with 1+1 long combs, each macrochaeta of all combs distinctly spaced apart from adjacent macrochaetae. Coxites IX of both sexes typical for the Heterolepismatinae, with large, prominent parameres. One pair of styli only (IX). Ovipositor of female simple.

Etymology. The genus name derives from the Latin word “maritimus” referring the proximity of known collection sites to the ocean combined with the suffix -isma, used for many silverfish. It is treated as grammatically neuter.

Remarks. When initially examined by the first author, the specimen did not immediately appear to belong to the Heterolepismatinae, however with due consideration, most

characters were generally in agreement with those associated with the Heterolepismatinae. Molecular data could not be obtained for this species due to the length of time the specimens had been in 70% ethanol. The character analysis places *M. coralinium* sp. nov. closest to the *H. stilivarians* group predominantly because both share the presence of macrochaetae rather than setae on the labrum, however the species share little else in common. The *stilivarians* group is currently under revision and the available molecular data places it quite distant from the remaining Australian species of *Heterolepisma* for which molecular data is available.

The new genus can easily be distinguished from all described Heterolepismatinae (except *H. dispar* – see below) by the following combination of characters: the presence of chaetotaxy on the anterior margin of the frons, the absence of branched papillae on the ultimate article of the maxillary palp, the presence of 3+3 combs on urotergite I, the presence of a medial comb on urosternite I, the very long 1+1 combs of eight or more spaced macrochaetae on urosternites II–VI, the number of pairs of styli (one pair in both sexes), the wide ultimate article of the labial palp and the much shorter urotergite X.

***Maritisma dispar* (Uchida, 1944) n. comb.**

Heterolepisma dispar Uchida, 1944: 185.

Heterolepisma dispar, a species inhabiting coastal cliffs from the Japanese Island of Honshu, appears, from the original description and illustrations, to share many of the unusual characters such as the macrochaetae along the anterior margin of the frons, the short urotergite X, the long, spaced urosternal combs and the long parameres. The chaetotaxy of urosternite I was not mentioned but the species shares so much of the unusual morphology of *H. coralinium* sp. nov. that it is likely to also possess a medial comb. Both species lack a glabrous anterior margin to the frons, both have a very broad ultimate article to the labial palp, urotergite X is greatly reduced and they have unusually long urosternal combs with widely spaced macrochaetae. These characters differentiate them from the remaining species with medial combs on urosternite I. However, the illustration of Uchida suggests that the pronotal collar is complete in *H. dispar*. This Japanese species is here provisionally transferred to the new genus.

***Maritisma coralinium* sp. nov.**

<http://zoobank.org/NomenclaturalActs/CC4C0649-D95F-42E5-8DE1-18BAA041F6A4>

Figs 169–207

Holotype ♂ (HW 1.14) (AM K.261124 K.261125 on two slides) CORAL SEA TERRITORY: Herald Cay (unspecified), Great Barrier Reef, 17.0°S 149.2°E, 7 September 1967. **Paratype**, juvenile ♀ (HW 0.84) (K.261252 K.261253 on two slides) CORAL SEA TERRITORY: North East Herald, 22.vi.1997, A. Anderson.

Diagnosis. This species can easily be distinguished from *H. dispar* in having one fewer pair of styli in the female and 2+2 combs on urotergite VIII (apparently 3+3 combs in *H. dispar* which would be very unusual), the shape of the thoracic sternites (apparently somewhat pointed in *H. dispar*), the much shorter penultimate article of the maxillary palp relative to the ultimate article (subequal in *H. dispar*).

Description

Appearance: Medium sized silverfish, thorax not wider than abdomen (Fig. 169) which only tapers slightly posteriorly from about the fourth abdominal segment; appearance when live unknown.

Body length: H+B 5.7 mm; HW 1.14 mm; thorax: length 1.8 mm or 0.32 H+B; width up to 1.5 mm with no great difference between the pro, meso- and metanota although the metanotum is the widest and the pronotum the narrowest, pronotum slightly longer than meso- or mesonota; antennae not complete 4.0 mm or >0.70 H+B; terminal filaments almost completely lost.

Pigmentation: Without pigment, possibly because of long time in alcohol. Paratype (K.261252) has some reddish-brown pigment around the eyes but otherwise appears to be without pigment.

Macrochaetae: Smooth, hyaline, apically bifurcate with truncated tips to each bifurcation (Fig. 170). Some macrochaetae on tibia, stout carrot-shaped. Some macrochaetae on tibia and tarsi appear slightly twisted, which is considered an artefact of the mounting medium as (e.g., Smith *et al.*, 2012).

Scales: Quite broad, hyaline, with unusually widely spaced subparallel ribs that do not surpass the margin of the scale (Fig. 171). Scales found on top of head, absent from clypeus and labrum as well as all cephalic appendages; present on all nota, all thoracic sterna, and the coxae but absent from remaining leg articles, present on all urotergites and urosternites, absent from styli and terminal filaments. Lanceolate and triangular scales not seen.

Head: Wider than long (Fig. 172), without distinct bushes. Frons projected forwards slightly in anterior corners; anterior margin with about 3+3 macrochaetae (lacking distinct medial gap) which join laterally with the rows of macrochaetae along the margin, running back to the eyes, with just a couple of macrochaetae above the eyes; peri-antennal groups ill-defined, of two macrochaetae located more mesad than the margin macrochaetae. Clypeus with longer macrochaetae laterally and across the face proximally, with small setae medially. Labrum (Fig. 172) with many macrochaetae distributed across the proximal half and some smaller setae in the anterior half. — Scape and pedicel of antennae (Fig. 173) both comparatively short, each with a subapical rosette of small macrochaetae and setae. First annulus of flagellum with very few setae; subsequent annuli with a rosette of small setae and some very short trichobothria, the divisions between the annuli difficult to discern in the slide mounted material. Most distal surviving intervals (probably about mid-antenna) (Fig. 174) divided into repeated patterns of four annuli, each with two rosettes of fine setae, rod-like basiconic sensilla may or may not be present (a vague impression of a basiconic sensilla was seen in the distal annulus of two intervals but were not seen with any confidence). — Mandibles short and robust (Figs 175, 176) but otherwise of a form typical for the Heterolepismatinae with well-developed molar and incisor areas; a group of about nine strong and short or thin and longer, apically bifurcated setae distally adjacent to the molar region and a bush of about 20 macrochaetae externally. — Maxilla (Figs 177, 178) with several thick apically bifurcate macrochaetae externally proximal to the palp; lacinia short and wide, with three strong teeth, one set further back than the other two, followed by about seven lamellate processes

and a row of five to seven setae, galea with one stronger seta proximally but otherwise with only short fine cilia or setulae; apical article of maxillary palp (Fig. 179) 4.6 times longer than wide (range 4.3–5.0) and 1.9 times longer than the penultimate article (range 1.4–2.3), the ultimate article without branched papillae but with a single sausage-shaped basiconic sensillum type C near the apex (although on the juvenile paratype K.377828 this sensillum looks more like a basiconic sensillum type B), last three articles of palp with fine setae only, two basal articles with subapical rosettes of slightly thicker setae. — Labium (Fig. 180) wider than long, postmentum with setae scattered irregularly across the anterior third, prementum with transverse and oblique groups of strong setae and with short setulae distally; apical article of labial palp, much wider than long (L/W 0.61), especially medially, with five papillae of the *aufgelöst* type arranged in a three plus two arrangement, the distal three being much larger than the other two, no other sensilla seen; covered with numerous fine short setae, those proximal and medial longer than those distal and/or lateral; penultimate article with three stronger setae medially.

Thorax: Pronotum (Fig. 181) with weak setal collar of short macrochaetae and some small setulae and cilia, chaetotaxy largely absent in medial region; setae of lateral margins lost, but consisting of marginal setae as well as setulae and two submarginal macrochaetae, one about one quarter the distance along the margin and the other about three quarters along the margin associated with the posterior trichobothrial area; on the left side there are two submarginal macrochaetae, the more mediad being smaller. Anterior trichobothrium about half way along the margin mediad of a marginal macrochaeta but otherwise without any special chaetotaxy (Fig. 182). The posterior trichobothrium mediad of a submarginal and a marginal macrochaeta with some two or three setulae posterior to this group (Fig. 183). Posterior margin with 1+1 single macrochaetae (absent on left side in holotype) each associated with two cilia (Fig. 184). — Mesonotum (Fig. 185) with similar lateral chaetotaxy to pronotum except two of the submarginal macrochaetae form combs of two at least on the right side (left side damaged); both trichobothrial areas are more posterior (Fig. 186) than on the pronotum, the anterior about $\frac{2}{3}$ along the margin, not associated with any macrochaetae; 1+1 posterior macrochaetae as in pronotum. — Metanotum (Fig. 187) similar to mesonotum except the trichobothrial areas even more posterior (Fig. 188).

Presternum narrow, with transverse row of strong macrochaetae (Fig. 189). All thoracic sterna with hyaline

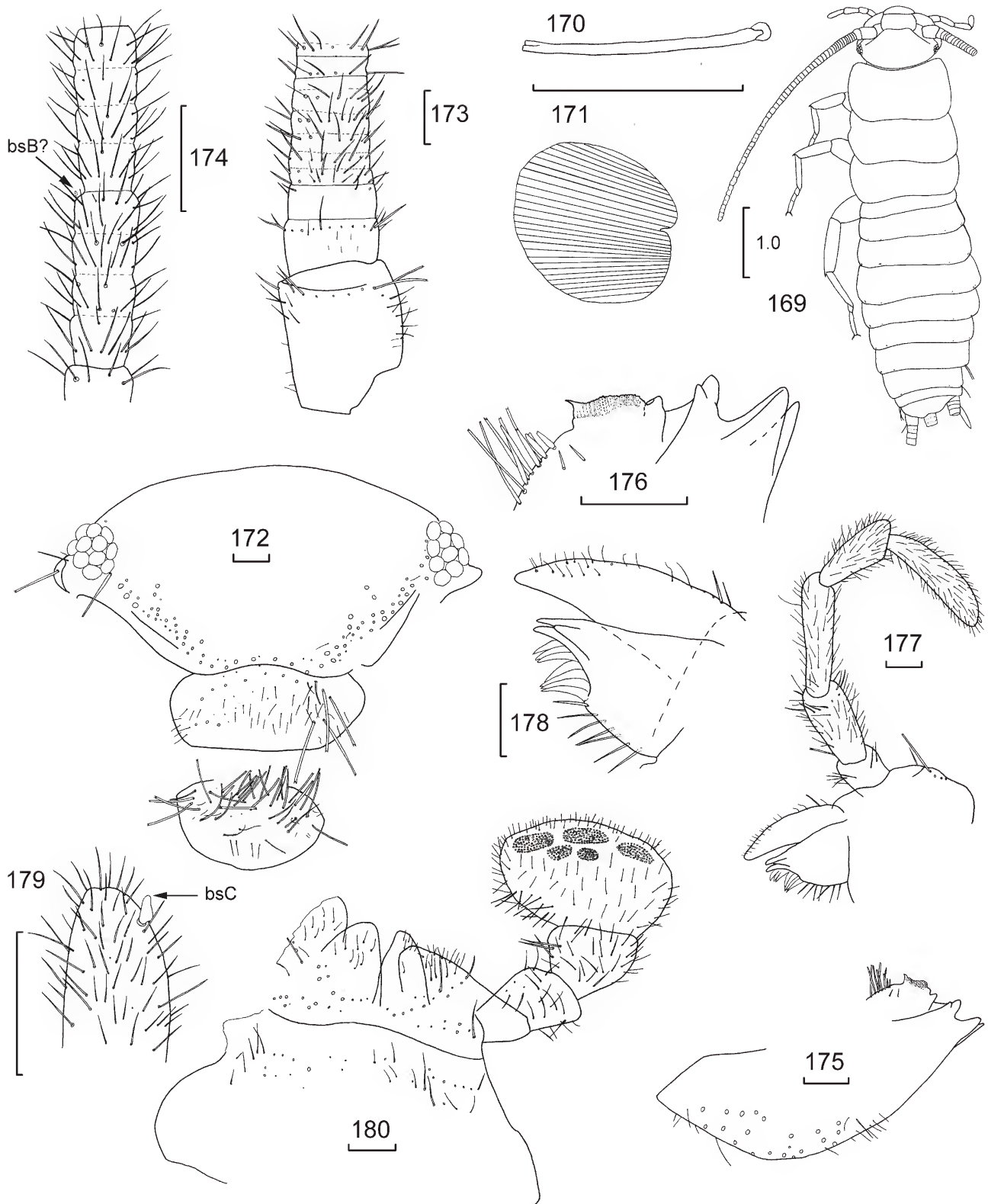
scales. — Prothoracic sternum (Fig. 189) subparabolic, about as wide at base as long (L/W 1.03), posterior two thirds of lateral margins with submarginal macrochaetae, often grouped into pairs. — Mesosternum (Fig. 190) sub-parabolic (L/W 1.13) with about 12 macrochaetae submarginally along the posterior third of the margin. — Metasternum (Fig. 193) apically rounded, about 1.25 times wider than long (L/W 0.81), distal third of lateral margins with submarginal rows of macrochaetae as well as some marginal setae and cilia, the small gap between the combs relative to the average length of each comb 0.62.

Legs (Figs 189, 191, 192, 194) becoming progressively longer and more slender with the tibia PI/PIII of 0.58 and the tarsi of PI/PIII of 0.69; tibia L/W ratio of legs of holotype PI 2.6, PII 3.1, PIII 4.2; tarsi L/W ratio PI 7.7, PII 8.9, PIII 11.8. Coxa of PI with comb of three strong macrochaetae near the anterolateral corners followed by many strong macrochaetae along the external margin, becoming more numerous distally; inner margin with three macrochaetae distally over the articulation and another seta subdistally near a long thin seta on the dorsal face. Trochanter with several setae. Femur ventrally with some macrochaetae along the posterior margin and another subdistally on the midline of the ventral face, distal anterior corner with one (?) macrochaeta, otherwise no obvious chaetotaxy along the ventral face of the distal end, ventral surface of femur with long setae. Tibia with a strong carrot-shaped macrochaeta distally as well as a few smaller strong setae, ventral margin with two short macrochaetae near the middle and another near the proximal end, dorsal or outer margin with one short pointed macrochaeta about one quarter the distance along the margin and another three quarters along; apical spur distinctly hooked (Fig. 191) and bearing two small setae; face of tibia also with setae. Tarsi of four articles, the basal tarsal article of PI longer than remaining articles together, bearing some stronger setae below; second article particularly short with two long setae, suture between third and fourth articles weak. Pretarsus with two long curved lateral claws and a much shorter straight medial claw. PII and PIII similar to PI except lacking the anterolateral comb on the coxae and with fewer macrochaetae in the posterolateral region; the relative length of the basal tarsal article is progressively longer, being about 63% of the total length on PIII. Tibia of both PII and PIII with more numerous stout macrochaetae along much of the length of the posterior margin

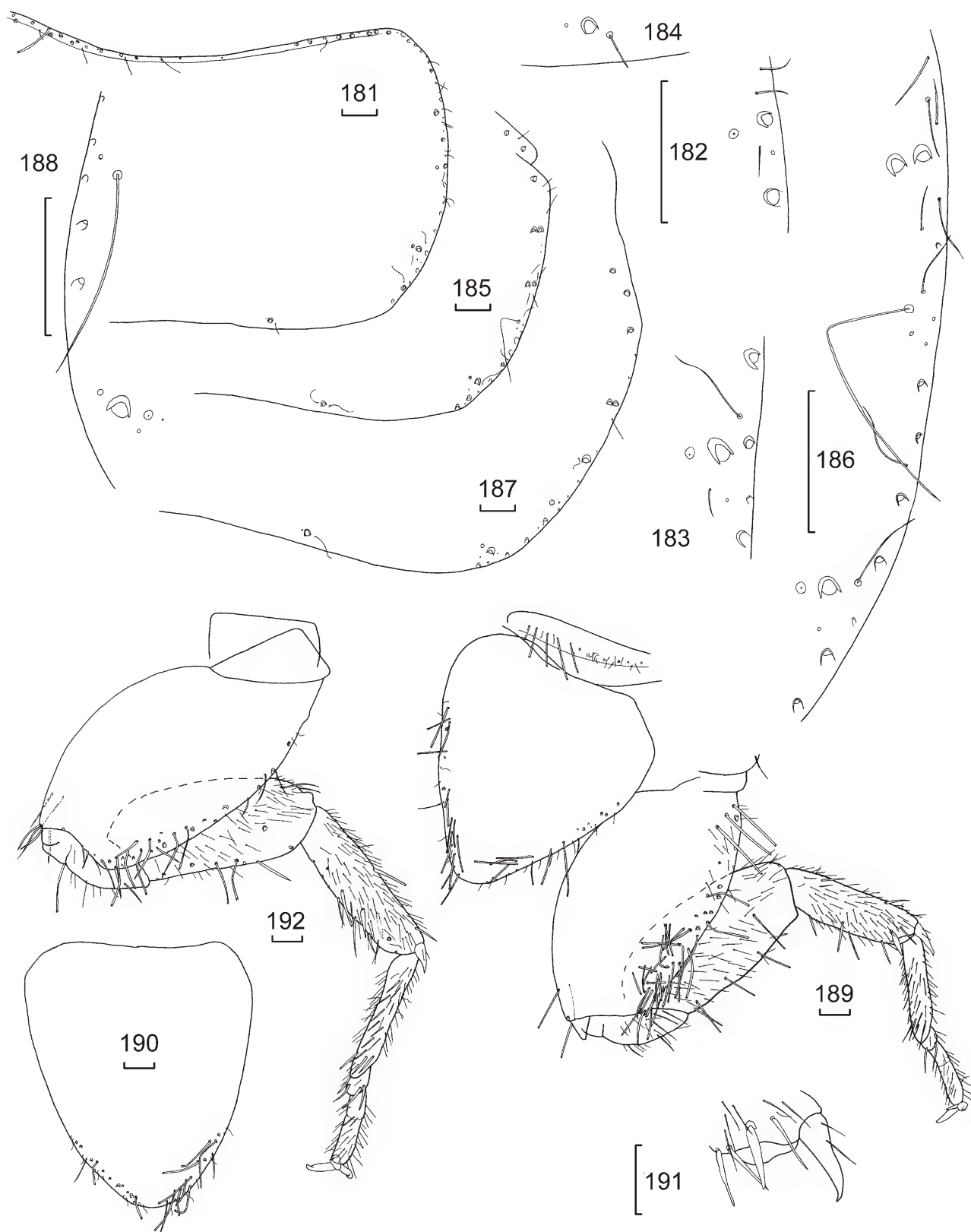
Abdomen: Urotergites I–VII with 3+3 small combs (Fig. 195), number of macrochaetae per comb as shown in Table 9,

Table 9. Number of macrochaetae per bristle comb—*Maritisma coralinium* gen. nov., sp. nov.

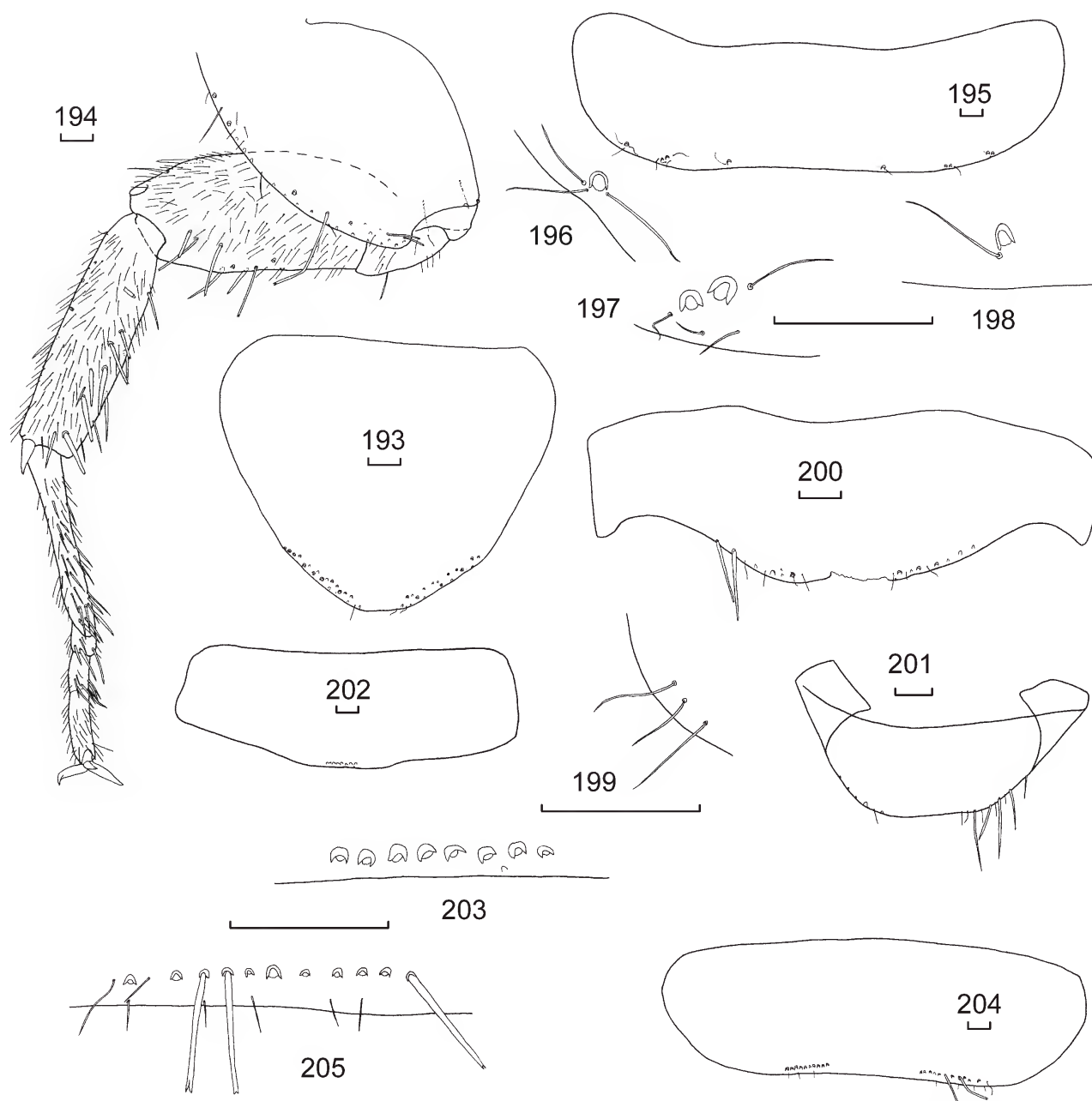
segment	urotergite			urosternite	
	lateral	sublateral	submedial	medial	lateral
I	1	1	1	8	—
II	1–2	2	1	—	8
III	2	2–3	1	—	8–10
IV	2	2	1	—	9–11
V	2–3	2	1	—	8–11
VI	2	1–2	1	—	8–12
VII	2	1–2	1	—	4–12
VIII	1–2	—	1	—	2–9



Figures 169–180. *Maritisma coralinium* gen. nov., sp. nov. holotype ♂ K.261124 K.261125 (169) habitus (terminal filaments lost); (170) smooth, apically bifurcate seta of setal collar; (171) scale from pronotum; (172) head, frons drawn separate from rest as it was folded back under the clypeus in the mounted material; (173) antenna, scape, pedicel and basal intervals of flagellum; (174) idem, most distal surviving interval showing possible basiconic sensillum (**bsB?**); (175) mandible; (176) idem, incisor and molar regions; (177) maxilla; (178) idem, lacinia and galea; (179) idem, apex of ultimate article of palp showing basiconic sensillum type C (**bs**); (180) labium. Scale bars = 0.1 mm unless otherwise indicated.



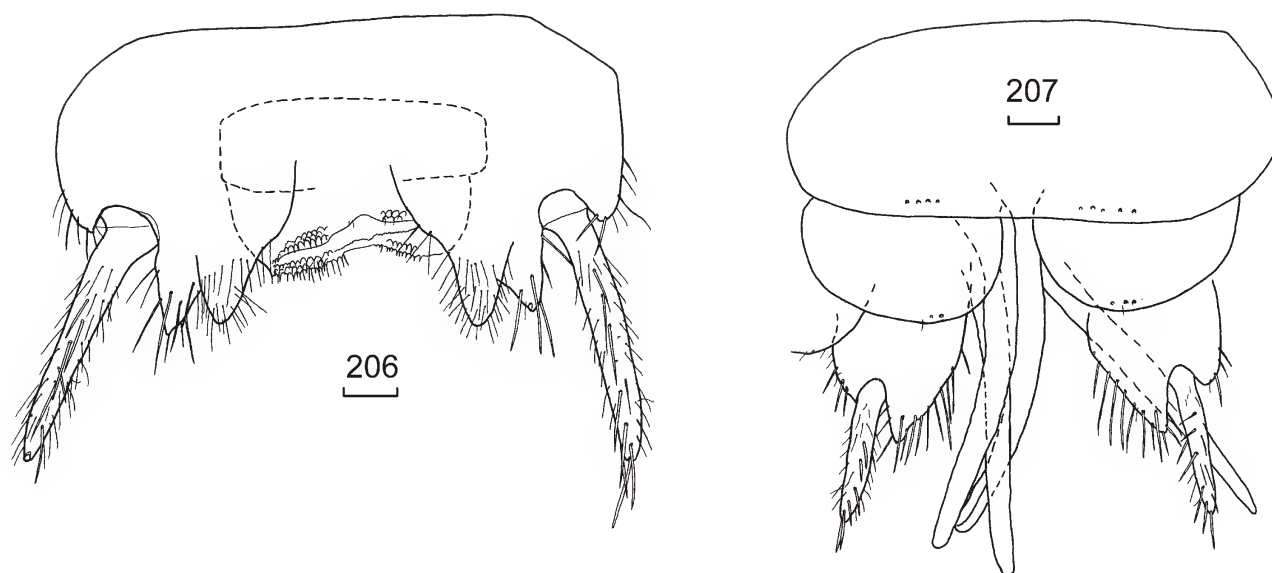
Figures 181–192. *Maritisma coralinium* gen. nov., sp. nov. holotype ♂ K.261124 K.261125 (181) pronotum; (182) idem, right anterior trichobothrial area; (183) idem, right posterior trichobothrial area; (184) idem, left posterior comb; (185) mesonotum, right side; (186) idem, trichobothrial areas, right side; (187) metanotum, right side; (188) idem, trichobothrial areas, left side; (189) presternum, prothoracic sternum and PI; (190) mesothoracic sternum; (191) apex of tibia of PI; (192) PII. Scale bars = 0.1 mm.



Figures 193–205. *Maritisma coralinium* gen. nov., sp. nov. holotype ♂ K.261124 K.261125 unless otherwise noted by specimen number (193) metathoracic sternum; (194) PIII; (195) urotergite II; (196) idem, left lateral comb; (197) idem, left sublateral lateral comb; (198) idem, left submedial comb; (199) urotergite IX, left infralateral comb; (200) urotergite X; (201) urotergite X of paratype K.261253; (202) urosternite I; (203) idem, medial comb; (204) urosternite IV; (205) right comb of urosternite VI. Scale bars = 0.1 mm.

each lateral comb associated with two to three cilia near the insertions and zero to four setulae nearer the margins, each sublateral comb associated with one to four cilia and zero to two setulae, each submedial comb of only one macrochaeta with a cilium on each side (Figs 196–198); urotergite VIII with 2+2 combs, lacking the sublateral comb; urotergite IX without combs but with three setulae in each infralateral corner (Fig. 199). Urotergite X (possibly slightly damaged in holotype) (Fig. 200) does not project posteriorly (L/W about 0.2) but is very similar to that of the juvenile female paratype (L/W 0.23, range 0.19–0.26); four or five macrochaetae on each side as well as some setulae (Fig. 201).

Urosternite I (Figs 202, 203) with comb of eight macrochaetae and one setula medially on slightly protruding region, urosternite II with 1+1 lateral combs each of eight macrochaetae (right comb missing on deformed part of posterior margin in holotype) and two marginal setulae, urosternites III–VIII (juvenile ♀ with combs of 2–3 macrochaetae on coxites VIII) with 1+1 lateral combs of four to twelve macrochaetae associated with a cilium at the laterad end and two to five setulae mostly located on the margin or between the comb and the margin but occasionally between the insertion points of the macrochaetae (Figs 204, 205). The distance between the lateral combs 1.5–2.1 times the width



Figures 206–207. *Maritisma coralinium* gen. nov., sp. nov. holotype ♂ K.261124 K.261125 unless otherwise noted by specimen number (206) coxites IX, penis and parameres; (207) sternite VII, coxites VII and IX of subadult female K.261253. Scale bars = 0.1 mm.

of these combs. The spacing between the macrochaetae of the combs is always quite wide.

Each coxite IX of ♂ short (Fig. 206), the internal process acute apically, a little wider at its base than long (L/W 0.8) and about 2.2–3.1 times longer than the external process; external and internal margins of internal process and external margin of outer process with some setae, with a few near the apex of the inner process fairly strong. Penis typical with numerous glandular setae apically, each set on a protuberance. Parameres almost as large as the inner processes with about 40 thin setae.

Only one pair of styli (Fig. 206) present (IX); each stylus with line of stronger setae along the length of the ventral margin. Styli IX in male holotype (excluding the apical macrochaetae) about two and a half times the length of the internal process.

Cerci in holotype largely damaged with the two remaining basal divisions lacking scales. In juvenile female paratype, the divisions are shorter than wide until the fifth division, the sixth division is divided into two annuli with larger macrochaetae only in the distal annulus, the seventh division is divided into three annuli, the eighth into four with trichobothria subdistally in the second and larger macrochaetae subdistally in the ultimate annuli (missing beyond here). The median dorsal appendage is similarly organised with shorter divisions basally and the fourth about as long as wide, the fifth and sixth are divided into two annuli and the seventh and eighth into four and the ninth into at least six annuli (broken beyond here).

Female: Known only from juvenile specimen (Fig. 207).

Habitat. Collected on a remote coral cay, over 300 km from the mainland of Australia, where many birds roost but there is no specific data on collection site on the label of the holotype.

Paratype collected in rotten wood and leaf litter of *Pisonia* [Nyctaginaceae].

Etymology. Named from the Latin noun for coral.

Discussion

Zoogeography. The subfamily Heterolepismatinae now contains 30 described species placed within two genera. Nine of these species are described from Australia or islands believed connected to mainland Australia by dry land at some stage in relatively recent geological history (e.g., Tasmania and Barrow Island). Twelve species are reported from remote islands. Smith (2017) illustrated the known distribution of the subfamily which appears to be Gondwanan (re-produced below). Many undescribed species are represented in Australian museum collections suggesting that Australia has a very rich fauna and may have been a key centre for radiation of the genus with subsequent dispersal to Africa, Vietnam, Japan, South America and numerous islands either via Gondwanan links or over oceans.

While a few species of Ctenolepismatinae are also found on remote islands, the Heterolepismatinae seem to be consistently found on islands, at least those of the Pacific and Indian Oceans. Though wingless, some aspects of the biology of silverfish may explain their success at traversing oceans (see summary of biology literature in Smith, 2017). Firstly, they may live for a few years so longer crossings are possible within their lifetime. They are polyphagous and able to digest cellulose so can survive on a wide variety of food. They can survive long periods without food (for months or even up to one year) and probably do not need to drink, as at least some Ctenolepismatinae have been shown to absorb moisture from the atmosphere through their rectum. Australian species of the genus *Heterolepisma* are generally collected sheltering within cavities in the bark of trees or within leaf litter accumulations. Such habitats are likely to contribute to rafts of vegetation washed out to sea following storms perhaps taking their silverfish inhabitants with them. Heatwole & Levins (1972) collected flotsam over three years in the vicinity of Puerto Rico and examined the fauna still alive, identifying 19 families of insects as well as pseudoscorpions, snails, spiders, mites, millipedes, isopods

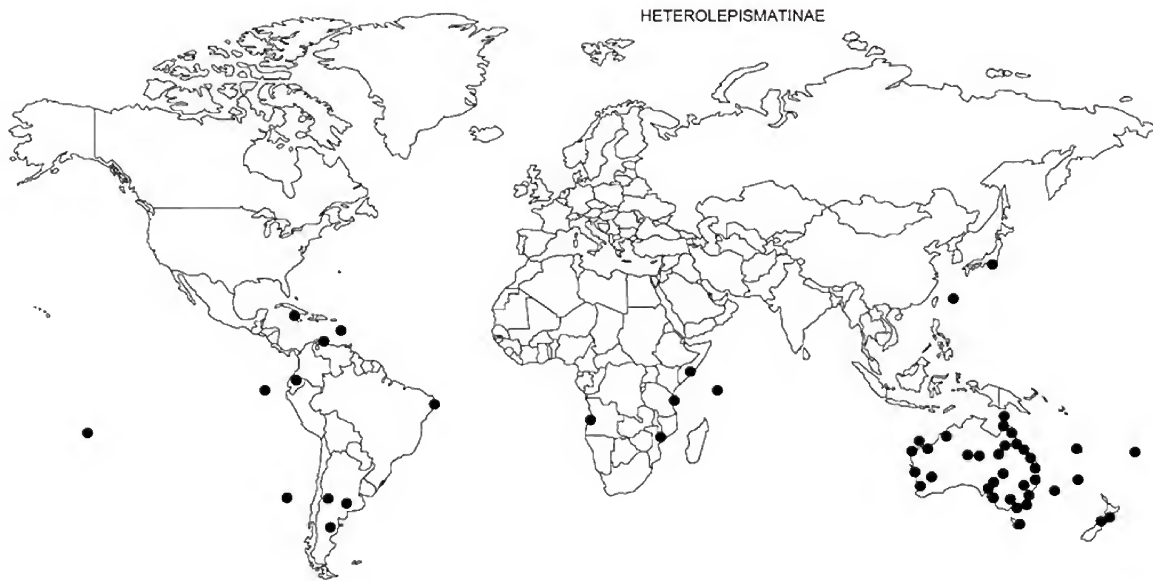


Figure 208. Known distribution of Heterolepismatinae species (from Smith, 2017).

and worms. No *Zygentoma* were found during their studies but the number of flightless taxa collected do suggest this as a probable means of transport.

Whatever the mechanism, it is clear that species of Heterolepismatinae are established on many islands and in several cases more than one species is present, even on very small land areas (<0.5 km²).

Phylogenetic relationships. Wygodzinsky (1967) and Mendes (1988) consider the characters of *Heterolepisma* to be plesiomorphic and thus an ancient lineage. However, the Gondwanan distribution of the Heterolepismatinae suggests it is more recent than subfamilies such as the Lepismatinae and Acrotelsatinae which show a much wider, probably Pangean distribution. Smith (2016) suggests that the characters of the Acrotelsatinae may be more ancient.

While much is still unknown regarding the Heterolepismatinae, molecular and morphological evidence is slowly accumulating that identifies several clades within the subfamily. One key character appears to be the absence of macrochaetae on the anterior margin of the frons. Most, if not all, such species also have lanceolate or triangular scales on the femora and tibia. Unfortunately, these characters have largely been overlooked in all but the most recent species descriptions.

Molecular data also suggest that a group of mostly undescribed species which includes *H. highlandi* Smith 2013 also form a distinct clade. This group has not yet been adequately examined morphologically but all species have just a single pair of styli in both sexes.

As more data are generated on the species of Heterolepismatinae it is becoming apparent that the genus *Heterolepisma* will probably need to be split into several genera. One challenge to this revision is the need to redescribe the type species of the genus, *H. pampeanum* Silvestri, from Argentina. While some type material still exists within the Museo di Entomologia “Filippo Silvestri”, Università degli Studi di Napoli Federico II, Portici, Italy, this material was collected from three widely separated localities and given our increasing understanding of the genus (e.g., Smith *et al.*, 2019) may well represent more than a single species. In any case, molecular data on the type species will probably only be obtained with fresh topotypic material.

Conservation. The two new species living on the Herald Cays (*M. coralinium* sp. nov. and *H. heraldense* sp. nov.) are at great risk from global warming. These islands are perhaps only a metre or two above current sea levels and are likely to be inundated as sea levels rise. Whether these two species are truly restricted to these islands or whether populations exist elsewhere is unknown.

Conclusion

The subfamily Heterolepismatinae appears to be quite successful at crossing large ocean barriers and establishing on very small islands. Recent molecular data and newly understood morphological characters suggest the genus will need to be split into several genera.

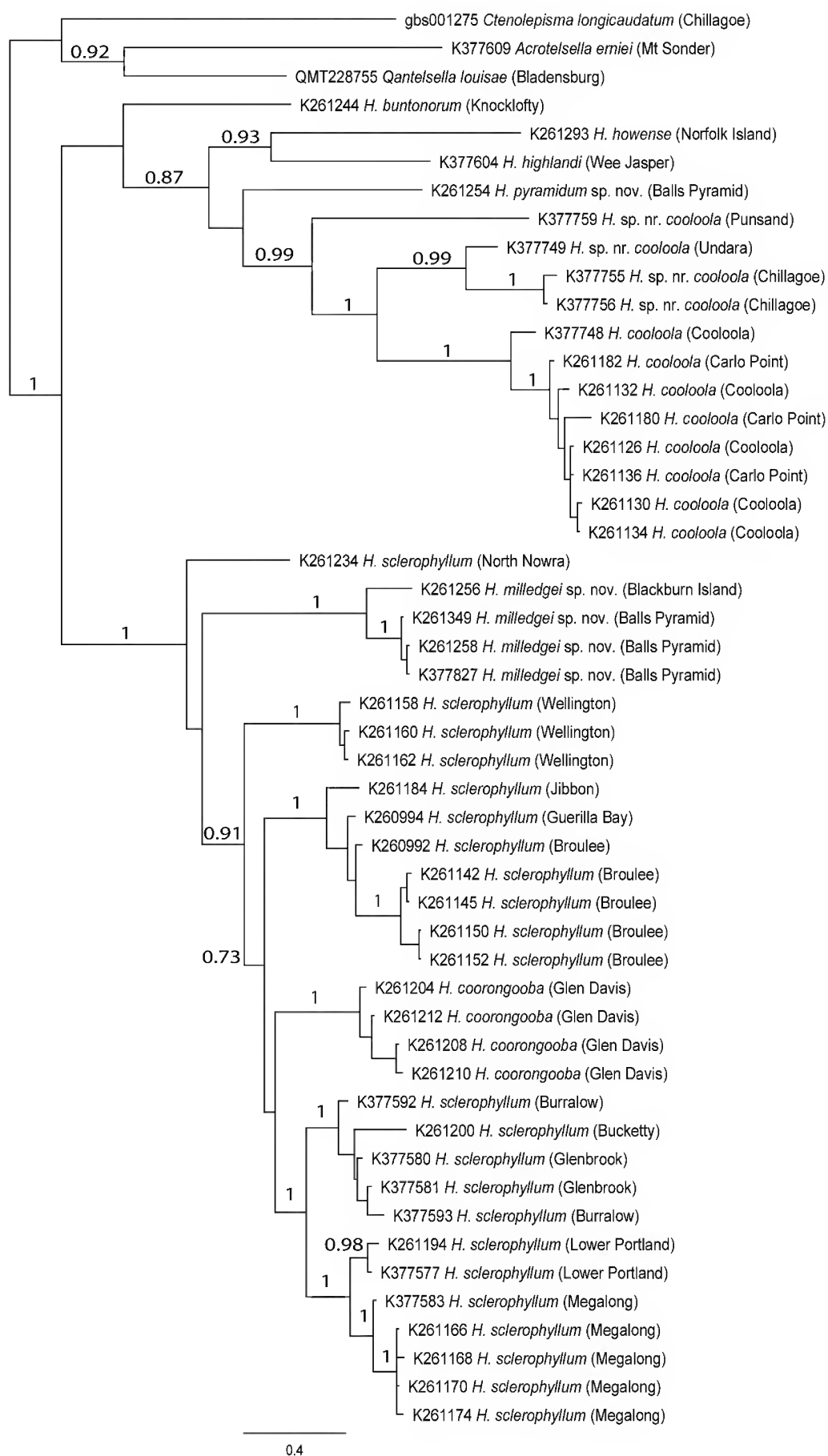


Figure 209. Bayesian tree for COI for some Heterolepismatinae on remote Australian islands.

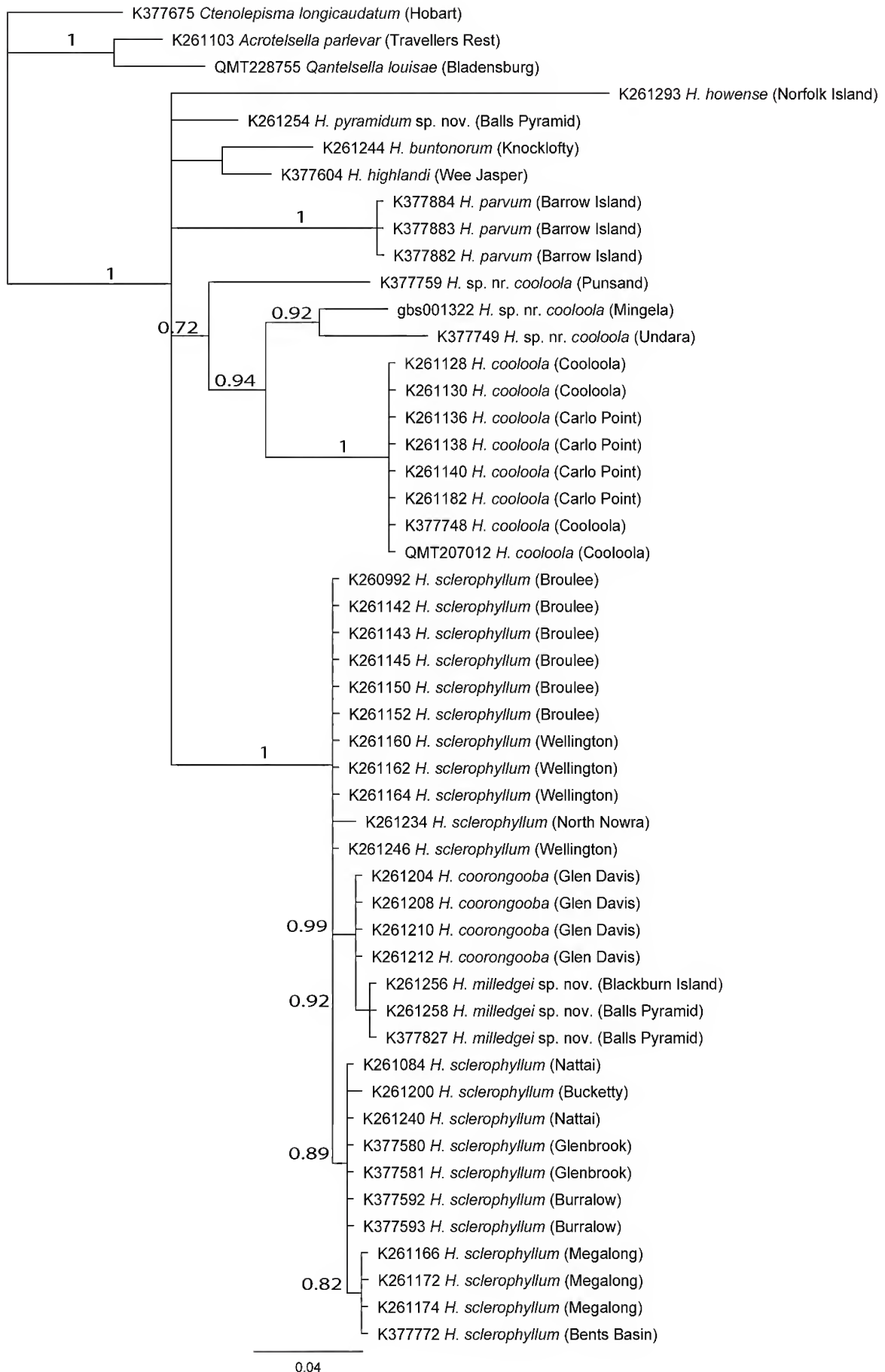


Figure 210. Bayesian tree for 28S for some Heterolepismatinae on remote Australian islands.

ACKNOWLEDGMENTS. We would like to thank Stephen Bunton, Hobart and Alice Wells, CSIRO, Canberra for collecting some of the material used to generate molecular sequences. Dr Luis Mendes, Lisbon, kindly re-examined type specimens of *H. tonga* and *H. mossambicense* for characters newly considered as important. We would also like to acknowledge support through the Australian Government Research Training Program Scholarship, via Federation University in Ballarat. Funding for the COI and 28S work was also provided by the Australian Museum Research Institute and an Australian Biological Resources Study Taxonomy Research Grant.

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